ECOLOGICAL MONOGRAPHS

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A STUDY OF ROOT DEVELOPMENT IN THREE SOIL
TYPES IN THE DUKE FOREST*

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INTRODUCTION

Studies of root distribution have recently occupied an important place in the field of ecological research. Much of the work, particularly in this country, has been concerned with herbaceous species and relatively little with woody species. In the southeastern United States few studies have been made that correlate measurements of environmental factors with root measurements of either herbaceous or woody species. Considering the correlation that exists between certain soil types and forest types in the Piedmont region, it seemed that a study of the root development of certain important woody species, within different soil types, would be desirable. Accordingly, the present study was undertaken. The object has been to contribute to existing knowledge of root development of seedlings of certain important woody species in three different soil types, and to determine as far as possible the specific edaphic conditions causing variations in root development.

This study of root development was made in the Duke Forest in Durham and Orange counties, North Carolina. Three soil types, namely the Congaree clay loam, Georgeville clay, and Orange loam, were selected for study after a careful consideration of their characteristics and of their vegetational relationships. Differences were evident at first observation, namely certain soil characteristics and the type of forest supported by each. Differences in composition and growth of forest stands appear to be associated with variation in soil type, and therefore present a problem in relation to soil properties. The specific stands on each of the soil types were chosen partly because of the various researches that had been and were being conducted in them. Thus a more complete picture of the conditions in each stand was anticipated, making the study of greater value than if it had been conducted independently of other studies.

This study was planned so as to obtain as far as possible, in addition to qualitative evidence, an amount of quantitative evidence sufficient to establish pertinent relationships between the three experimental areas.

To determine similarities and differences in the edaphic conditions of the three sites, certain measurements were made. Physical properties of the soils were measured by determinations of waterholding capacity, air capacity, volume-weight, wilting percentage, field percolation rate, mechanical analysis, soil aggregation, soil air space, soil porosity, and soil atmosphere. No measurements of rainfall, evaporation or soil acidity were attempted as a direct part of this study, but the data were obtained from records kept by the Duke Forest Staff. To ascertain the relative soil moisture conditions of the three sites, determinations were made at appropriate intervals throughout

the spring and summer of 1936, from May 5 to August 6.

The species chosen for study were white oak (*Quercus alba* L.), post oak (*Q. stellata* Wang.), blackjack oak (*Q. marilandica* Muench.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muench.), northern red oak (*Q. borealis* Michx. f. var. *maxima* (Marsh.) Ashe), loblolly pine (*Pinus taeda* L.), red cedar (*Juniperus virginiana* L.), yellow poplar (*Liriodendron tulipifera* L.), dogwood (*Cornus florida* L.), red gum (*Liquidambar styraciflua* L.), sourwood (*Oxydendrum arboreum* (L.) DC.), red maple (*Acer rubrum* L.), and downy viburnum (*Viburnum affine* Bush var. *hypomalacum* Blake).

Since seedlings of the above species did not occur naturally on all three sites, seeds of all species except red maple and downy viburnum were planted in each. Data were obtained on germination and on survival of seedlings. Most of the seedlings thus established, as well as those occurring naturally, were later excavated. Observations as to injury from natural causes and drawings, weighings, and measurements were made.

The writer wishes to acknowledge the assistance of Dr. C. F. Korstian, under whose direction this research was done and whose patient and helpful criticism rendered its completion possible. Thanks are due Dr. P. J. Kramer for helpful criticism, and for suggestions and assistance in the use of soil atmosphere apparatus. The author extends thanks to the various members of the Department of Botany and School of Forestry who have contributed their time and advice toward the completion of the research, especially to Dr. H. J. Oosting, Dr. H. L. Blomquist, Dr. H. S. Perry, and Dr. T. S. Coile. Various equipment was used that belongs to the Department of Botany of Indiana University, Bloomington, Indiana and to the School of Forestry of Duke University.

EXPERIMENTAL AREAS

The general features of the locality which includes the three sites chosen for this study are described by Korstian and Maughan (1935). The soils of the locality are discussed by Perkins *et al.* (1924) and Vanatta *et al.* (1921). The bottomland soils are recent alluvium while all of the upland soils are residual. Differentiation of the soils has been controlled mainly by character of the parent rock, topographic position, and by erosion.

The three areas chosen for this study are on the Congaree, Georgeville, and Orange soil series. In addition to their soil characteristics the areas differ in most respects in their location, history, and vegetational relations. Therefore, each of the experimental areas will be described separately. Korstian and

Coile (1938) give other data, including photographs, concerning these three areas in which their trenched plots 7, 5, and 4, respectively, were located.

AREA 1: CONGAREE CLAY LOAM

The area chosen on this soil was located in the Durham Division of the Duke Forest. It occupied the bottomland along Browning's Branch about 300 yards south of Erwin Road and was near permanent sample plots 43 and 44. Part of the study was made in Stand 2, Compartment 32, and the remainder just across the stream in Stand 15, Compartment 23. The experimental area was entirely within an uneven-aged stand of the red gum-yellow poplar forest type which occupied most of the bottomland in the vicinity. The bottomland was subject to inundation but between overflows was moderately well drained. Variable amounts of alluvium were deposited with each inundation.

The stands were almost pure red gum and yellow poplar. The most important associated species were sycamore (*Platanus occidentalis* L.), river birch (*Betula nigra* L.), red maple, and green ash (*Fraxinus pennsylvanica* Marsh. var. *lanceolata* (Borkh.) Sarg.). Occasional representatives of black oak, blackjack oak, white oak, beech (*Fagus grandifolia* Ehrh.), elms (*Ulmus* spp.), and red cedar were also present. Reproduction of the dominant species and blue beech (*Carpinus caroliniana* Walt.), hop-hornbeam (*Ostrya virginiana* (Mill.) Willd.), dogwood, redbud (*Cercis canadensis* L.), and sourwood constituted most of the understory. Among the most important shrubs were downy viburnum, *Lonicera japonica* Thunb., and *Smilax rotundifolia* L. The herbaceous vegetation was composed of a large number of species. Their estimated total coverage was less than 50 per cent. The herbs that are most abundant include the following: *Podophyllum peltatum* L., *Carex* spp., *Poa autumnalis* Muhl., *Uvularia perfoliata* L., *Galium circaezans* Michx., and *Glyceria striata* (Lam.) Hitchc.

The soil had developed only an A₁ horizon. It consisted of a brownish clay loam that was quite plastic when moist, extending to a depth of 1.5 to 2.5 inches. From that depth down to 6.5 to 10.0 inches was located a layer of structureless sandy loam, lighter in color due largely to a lower organic matter content. Below the latter layer were generally found stratified layers of sand and sandy loam. At 18 to 20 inches residual soil was found, or, up to three or more additional feet of alluvial soil and then residual soil. The entire soil was rather loose and contained small mica flakes.

AREA 2: GEORGEVILLE CLAY

This site was located in Stand 2, Compartment 15 of the New Hope Creek Division of the Forest, near permanent sample plots 36 and 37. The stand belonged to the white oak-black oak-red oak forest type. The area was well drained, being located on a gently rounded upland area located between two small streams.

The forest was composed largely of white oak, northern red oak, southern red oak (*Quercus rubra* L.), scarlet oak, black oak, hickory (*Hicoria* spp.), and red maple. Dogwood, hop-hornbeam, sourwood, and redbud made up most of the understory. *Polycodium neglectum* Small and *Vaccinium tenellum* Ait. in scattered clumps, downy viburnum, and *Vitis rotundifolia* Michx. composed most of the shrubby layer. *Ascyrum hypericoides* L., *Hieracium Gronovii* (L.) Kuntze, *Lespedeza repens* (L.) Bart., *Meibomia nudiflorum* (L.) Kuntze, and *Panicum Boscii* Poir were the most important herbaceous species. The estimated total coverage of the low shrubs and herbaceous vegetation together was no more than 25 percent.

The Georgeville soil profile was well developed. The A₁ horizon was a light-brown, stony clay, passing at 0.5 to 1.5 inches into the A₂ horizon, a reddish-yellow, rather compact, stony clay exhibiting a crumb structure and extending to a depth of 5.0 to 7.0 inches. The B horizons were dark red, brittle clays, exhibiting bright surfaces when moist soil was broken. The B₁ gradually graded into the B₂ horizon, the latter being slightly darker in color and more compact. The C horizon occurred at a depth of 24 to 40 inches. It was a granular clay whose color was yellowish-red with lighter mottlings.

AREA 3: ORANGE LOAM

This study area was located in Stand 1, Compartment 15 of the New Hope Creek Division of the Forest. The forest type was post oak-blackjack oak. In addition to post oak and blackjack oak which made up the dominant stand, there were scattered groups or individuals of loblolly pine, shortleaf pine (*Pinus echinata* Mill.), black oak, and red cedar. Permanent sample plots 34 and 35 were located in this stand. Near these plots in the naturally open forest was the area chosen for study in the Orange loam soil type. The area was upland but was poorly drained, the slope being too gentle to allow proper drainage.

Scattered individuals of downy viburnum occurred within the area, but few other shrubs were to be found. The herbaceous vegetation, however, was rather abundant having an estimated coverage of around 75 percent. The most abundant herbs were: *Danthonia spicata* (L.) Beauv., *Agrostis perennans* (Walt.) Tuckerm., *Andropogon scoparius* Michx., *Panicum* spp., *Aristida dichotoma* Michx., *Sericocarpus linifolius* (L.) BSP., *Phlox nivalis* Todd., *Lespedeza frutescens* (L.) Britton, and *Acalypha gracilens* A. Gray.

The A₁ horizon of the soil was a light-gray, floury, stony loam, underlain at 1.0 to 2.0 inches by a dull-yellow loam (A₂ horizon) which extends to a depth of 7.0 to 9.0 inches. The B horizon was a dingy-yellow, extremely plastic, waxy, impervious clay. The C horizon which began at 17 to 20 inches was a friable, mixed greenish and yellowish clay.

METHODS OF STUDY

In order to provide for seedlings of each species in each of the three experimental areas, two seed

plots were established in each. The plots were 4 by 5 feet and were covered with cages constructed of one-fourth-inch mesh wire screen to prevent disturbance as far as possible, especially by rodents. Twelve rows for seeding, one for each species, were laid out in each plot. The seeds of all species were placed in the rows during the first ten days of November, 1934; except for white oak and post oak which were planted at the time of acorn fall in October 1934. The number of seeds planted are shown in Table 8. The plots were undisturbed with the exception of the slight movement of soil during seeding and the removal of herbaceous and shrubby ground cover to allow the wire cages to be placed tightly over each seeded area.

The total number of seedlings of each species in each plot and their average heights were recorded on June 1, and October 1, 1935 and again on May 20, 1936.

ROOT DEVELOPMENT

To determine the extent of root development of seedlings, excavations of entire root systems were made. A small trowel and a knife were used. Care was exercised so that practically every root system was removed intact. When a drawing of a root system was to be made each part was outlined as that part was uncovered. All excavated specimens were brought into the laboratory and measurements and oven-dry weights of total plant, root, and top were made of each, and the averages for each species and site were determined.

Laing (1932) found that throughout a year there are variations in ratio of weight of shoot to weight of root in seedlings of three coniferous species. He states that it is likely that shoot growth and root growth alternate. Reed (1939) found that in the case of loblolly pine and shortleaf pine in the Duke Forest there was an initial surge of both root and shoot growth in April and May, after which these two growing regions apparently alternate in their periods of activity. To minimize possible effects of such variations on data in the present study, all excavations of seedlings of a given species were made as near the same date as was possible. Those in the seed beds were begun early in March, 1936, and were completed by the middle of April, 1936. Drawings and careful observations of each seedling were made at the time of excavation. Excavations of naturally seeded specimens were made in the late autumn of 1936 and in May, 1937, and drawings of representative root systems were made.

The excavations made in the late autumn of 1936 were of seedlings that had completed their first summer's growth. Observations concerning growth of seedlings indicated that little if any growth of roots or tops was made from that time until the next March. Therefore the data from this group of seedlings were compiled with those from seedlings excavated in the spring from the seed beds, as it could reasonably be assumed that they were at the same stage of development.

The excavations in May, 1937 were of 1- and 2-year-old red maple and downy viburnum seedlings and of 2-year-old white oak seedlings. This group of excavations was terminated when a search showed that there were no more seedlings of any species from which sufficient, pertinent data could be obtained.

Drawings of the root system serve as qualitative data on root development. Quantitative data were obtained by weighings and measurements of uninjured seedlings. In the field depth of penetration of main radicle, root diameter, and shoot height above ground level were measured, after which each specimen was placed in a numbered, air-tight can. In the labatory each seedling was carefully washed free of all soil particles, its drawing completed, and the total length of all secondary roots measured by means of dividers.

After drawings and measurements were completed, seedlings were dried in an oven at 105° to 110° C. for 36 hours. Leaves, when present, were removed at the abscission layer and discarded. Each seedling was removed to a desiccator and later weighed. The top was carefully cut from the root; in the oaks the point of separation was made at the cotyledonary sears and in the other species at the point of greatest basal swelling. The weights of top and root were then determined. All weighings were made at least to within accuracy of 0.001 gram.

SOIL FACTORS

Following preliminary examination with a soil auger three locations on each experimental area were selected as typical. At each location a well was dug, 6 feet long and from 2.5 to 5 feet deep, with the center of the broad face four feet from some tree of 5 to 9 inches in diameter at breast height. Profile maps were made for each well showing the soil horizons and location of roots by size classes on the vertical face next to the tree.

Three sets of soil samples were taken from each of the three areas. One set was collected in loose condition from soil wells, two quarts being taken from each horizon in each well. A second set was obtained from each horizon by means of a soil sampler (Coile, 1936) that was designed to obtain samples of undisturbed soil for the determination of volume-weight, air capacity, and water-holding capacity. Similarly, a third set was obtained by means of a soil sampler devised to take samples of undisturbed soil for making determinations of wilting percentage.

Surface samples in the second and third sets were taken at 4-foot intervals at a typical location in each experimental area. The points of intersection of lines at right angles in the form of a Latin square served as locations around which a sample and duplicate, if needed, were taken for each set.

The sub-surface soil samples were taken as soil wells were dug. In each well soil was removed to desired depth for sampling (2 inches, 10 inches, and 24 inches). At regular intervals across the exposed surface four samples for set two and three samples for set three were taken.

The first set of samples from soil wells was brought into the laboratory, dried, and crushed with a wooden

rolling pin so as to break up the soil aggregates and enable the soil to pass through a 2 mm. sieve. Soil particles that did not pass through the sieve openings were classified as gravel. The soil that passed through the sieve was then thoroughly mixed and all but one quart of a sample was discarded. In each soil type composite samples were then made for each horizon by combining samples from the three wells. In the Congaree soil only the upper three horizons were composited. The composite samples were used for mechanical analyses.

Bouyoucos' (1934, 1935) hydrometer method and a modification of Olmstead's (1930) pipette method were used in making mechanical analyses in duplicate. The textural class for each horizon was determined by the use of Davis and Bennett's (1927) equilateral triangle method. A modification (aggregate) of Bouyoucos' (1929) method was used in the determination of soil aggregation. The only difference from the usual hydrometer method (dispersed) was the omission of any mechanical means of stirring. The difference between these results and those obtained by the dispersed method was used to indicate aggregation in each soil fraction.

The second set of samples of undisturbed soil were brought into the laboratory, the top lid of each sampler removed, and a wire screen containing a filter paper placed on the top of the cylinder. It was then turned over, the other lid removed, and the cylinder submerged in water and allowed to soak for 48 hours. At the end of that time the cylinders were covered on top by a lid, turned over under water, then taken out, the excess water wiped off, and then weighed immediately. They were placed on a sand substratum with the wire screen down, uncovered, and allowed to drain for one hour, at the end of which time they were weighed again. The cylinders were drained and weighed a successive number of times at one-hour intervals until the loss of weight proceeded at an almost constant rate and very slowly. When that condition was reached, it was assumed that practically all of the gravitational water had drained from the samples. This obtained in almost every case at the end of the second hour. After draining for 12 hours the samples were dried to constant weight in a thermostatically-regulated oven at temperatures between 105° and 110° C.

Water-holding capacity was calculated on the basis of difference between oven-dry weight of the sample and the weight immediately after gravitational water had been drained out. It was expressed both on a volume basis and as a percentage of the oven-dry weight of the soil sample. The air capacity was considered to be equal to the volume of gravitational water. Volume-weight was expressed numerically as the oven-dry weight of the sample divided by the volume (600 cc.) which it occupied.

The third set of samples was obtained in cardboard containers that had been boiled in paraffin to make them moisture proof. The procedure for the determination of lower limit of available soil moisture as outlined and discussed by Briggs and Shantz (1911,

1912b) was used as a basis for determination of wilting percentage. Oats (*Avena sativa* L.) were used as phytometers. The procedure followed is given by Duncan (1939).

The field percolation rates were obtained from studies (unpublished) made by Coile and Korstian. They were determined by a modification of the method used by Auten (1933). Cylinders 10 inches in length with an inside diameter of 1.6 inches were used. When pushed into the ground up to the collar that was one inch from the lower end, each has a capacity of 305 cc. Percolation measurements were made at the intersections of lines at right angles in the form of a Latin square. The percolation cylinders were placed in the surface soil three feet apart and four 1,000 cc. cylinders and one 100 cc. cylinder filled with water. Each percolation cylinder was quickly filled with water from that measured out and kept full for ten minutes. At the end of that time the total amount of water poured in was determined. The rate of percolation per minute was then determined.

Measurements of soil porosity and soil atmosphere (CO_2 and O_2 content of soil air) were made with a portable apparatus consisting of three units: a soil sampler, a soil atmosphere sampler, and a gas analysis apparatus. The equipment and methods are modifications of those described by Goldsmith (1924). Complete sets of determinations on all three experimental areas at the surface, 8 inches, 12 inches, and 24 inches were made in April, 1935 and October, 1935.

Soil samples were obtained by the soil sampler. Air samples were taken from these and then transferred to a specially constructed, portable, field, gas analysis apparatus and analyzed for O_2 and CO_2 as suggested by Haldane and Graham (1935) in their directions for manipulation of this apparatus.

The series of soil moisture determinations in the spring and summer of 1935 were made from samples taken near three fixed points in each experimental area. Samples were taken from the four upper horizons, 0-1.5 inch, 2-5 inches, 10-13 inches, and 23-25 inches (the C horizon in Orange soil), those from the two upper depths by means of a garden trowel and from the two lower depths by means of a soil auger. The samples were placed in air-tight, numbered cans and later weighed, dried in an oven (105° to 110° C.), and reweighed. Their moisture content was calculated on the basis of oven-dry weight. Percentage of available water in the soil was considered to be the difference between wilting percentage and field moisture content.

STATISTICAL METHODS

When results were treated statistically, the standard deviation of each mean was determined (standard

$$\text{deviation} = \sqrt{\frac{Zd^2}{n-1}}, \text{ where } Zd^2 \text{ is the sum of the}$$

squares of the deviation of each variant from the mean and n equals the number of variants) in order to get a measure of scatter of the variants from which the mean was determined.

When the significance of the difference between means was tested, calculations were made in the following manner: The standard error of each mean was determined from the standard deviation (standard

$$error = \frac{standard\ deviation}{\sqrt{n-1}},$$ where n is the number of

variants) so that it would be possible to define the limits within which variations of the mean occur on account of conditions which are not within control. The standard error of the difference was determined (standard error of difference $= \sqrt{(S.E._x)^2 + (S.E._y)^2}$, where $S.E._x$ is the standard error of the mean of x, and $S.E._y$ that of y). The difference between the means was divided by the standard error of the difference. The value (t) was used to determine the probability (P) according to the table for P values as given by Fisher (1936). All differences between means that are not significant at the 0.05 level are not considered to be statistically significant.

PRESENTATION AND DISCUSSION OF RESULTS

The results of the study of edaphic conditions will be discussed so as to bring out the similarities and differences in the soils. From these differences the specific soil conditions which might be important in causing variations in root development can be more easily determined.

RESULTS OF THE STUDY OF EDAPHIC ENVIRONMENTS

SOIL ANALYSES

The results of mechanical analyses of Congaree, Georgeville, and Orange soils as determined by the pipette method are presented in Table 1. On the basis of texture of the A_1 horizon the Congaree soil is classed as a clay loam, the Georgeville as a clay,

TABLE 1. Results in percentage of oven-dry weight of mechanical analyses of Congaree, Georgeville, and Orange soils determined by the pipette method.

Horizon	Depth in Inches	Gravel	Total Sands	Silt	Clay	Colloids	Textural Grade
CONGAREE SOIL							
A_1.....	0–2	None	38.42	37.81	23.77	15.68	Clay Loam
2.......	2–7.5	None	57.75	24.45	17.00	14.74	Sandy Loam
3.......	7.5–19	Trace	58.21	25.49	16.30	11.54	Sandy Loam
4.......	19–25	Trace	84.80	8.81	6.39	4.26	Sand
5.......	below 25	None	57.36	27.78	14.86	10.32	Sandy Loam
GEORGEVILLE SOIL							
A_1.....	0–1.2	27.96	29.33	38.11	32.56	21.60	Clay
A_2.....	1.2–6	22.78	27.85	37.22	34.93	26.00	Clay
B_1.....	6–20	9.32	10.77	16.51	72.72	70.53	Clay
B_2.....	20–33	4.85	9.15	22.36	68.49	64.96	Clay
C.......	below 33	Trace	17.05	31.69	51.26	41.98	Clay
ORANGE SOIL							
A_1.....	0–1.5	4.78	40.64	43.98	15.38	11.02	Loam
A_2.....	1.5–8	27.07	42.94	38.76	18.30	15.46	Loam
B_1.....	8–14	3.18	18.71	30.39	50.90	46.38	Clay
B_2.....	14–19	1.47	21.51	30.67	47.82	40.80	Clay
.....	below 19	1.79	35.98	34.00	30.02	26.36	Clay

and the Orange as a loam soil. The soils are described in more detail by Duncan (1939).

As determined from the mechanical analyses of the Congaree, Georgeville, and Orange soils made by Bouyoucos' aggregate and dispersed method there was little aggregation of any of the soil fractions in the Congaree soil except in the A_1 horizon. However, in the Georgeville soil there was an indication of considerable aggregation, particularly in the B horizons which had high contents of the smaller soil fractions. There was some aggregation in all horizons of the Orange soil. The amount was generally much less than in the corresponding horizons of the Georgeville soil and was more than in the corresponding horizons of the Congaree soil except for the A_1 horizon.

SOIL MOISTURE CONDITIONS

Determinations were made of soil moisture conditions and of a number of related soil factors. Statistical treatments were made only on the results of the determinations of water-holding capacities, permanent wilting percentages, and field percolation rates.

Water-holding Capacity—The results of determinations of the water-holding capacities of the three soils at four depths are presented in Table 2. Each depth was located in a different horizon as reference to Table 1 will indicate. In each horizon the differences between the means of the three soils are all significant except between the Congaree and Orange at 10 to 12 inches on a volume basis. Determinations of water-holding capacity and other factors were omitted at 23 to 25 inches in the Orange soil because attempts to obtain samples in place were unsuccessful due to the compact, brittle nature of the soil at that depth.

All of the percentages determined on a volume basis were larger than those determined on a dry-weight basis because the weight per unit of volume was greater than unity as can be seen from the volume-weight values given in Table 2. It should be noted that the water-holding capacity of the surface horizon was generally as high or higher than the lower horizons to each of the three soils. Also the water-holding capacity of the Orange soil at all depths was generally relatively lower than those of the other two soils at the same depths.

Field Percolation Rates—The field percolation rates of the surface soils give valuable information as to the relative amounts of water passageways that existed in each soil. They also indicate the relative porosity of each soil. Slater and Byers (1931) found that the field percolation rate of a soil was governed more by the water passageways it contains than by character or volume of pore space of the soil mass. Coile (1935) found that waterways formed by soil-animal activity and decayed roots were more important than cleavage planes and pore space.

Data obtained in 1933 and 1934 by Coile and Korstian give values for the average percolation rates per minute for ten-minute periods of infiltration for the three soils. The percolation rates per minute were: Congaree, 41 ± 4.3 cc.; Georgeville, 198 ± 16.8

TABLE 2. Mean water-holding capacities expressed in percentages on dry-weight and volume bases, mean air capacities expressed in percentages of soil volume, and mean volume-weight, with the standard error of each mean, for the Congaree, Georgeville, and Orange soils at depths indicated.

	Congaree	Georgeville	Orange
Surface (0-2 inches)[1]			
Water-holding Capacity			
Dry-weight basis	42.62 ±0.76	38.14 ±1.15	32.08 ±0.87
Volume basis	48.22 ±0.44	45.46 ±0.76	39.81 ±0.40
Volume-weight	1.135 ±0.015	1.203 ±0.027	1.263 ±0.023
Air capacity	6.68 ±0.40	7.83 ±0.45	8.15 ±0.37
2-4 Inches[2]			
Water-holding Capacity			
Dry-weight basis	34.32 ±0.84	28.65 ± .069	23.96 ±0.78
Volume basis	44.36 ±0.45	39.42 ±0.56	35.80 ±0.89
Volume-weight	1.273 ±0.012	1.381 ±0.021	1.499 ±0.017
Air capacity	4.97 ±0.49	7.30 ±0.36	7.42 ±0.49
10-12 Inches[2]			
Water-holding Capacity			
Dry-weight basis	28.63 ±0.91	39.72 ±0.77	26.85 ±0.87
Volume basis	39.76 ±0.92	48.05 ±0.79	42.41 ±1.20
Volume-weight	1.393 ±0.014	1.212 ±0.019	1.582 ±0.011
Air capacity	5.18 ±0.36	5.15 ±0.37	1.72 ±0.14
23-25 Inches[2]			
Water-holding Capacity			
Dry-weight basis	30.32 ±0.99	41.34 ±1.11	....
Volume basis	42.47 ±0.88	50.27 ±0.66	....
Volume-weight	1.414 ±0.047	1.214 ±0.005	....
Air capacity	6.83 ±0.83	4.48 ±0.37	....

[1] 20 determinations on each area.
[2] 12 determinations on each area.

cc.; and Orange, 8.2 ± 1.3 cc. All differences between means were statistically significant. It is evident that the relative percolation rates of the three surface soils were increasingly greater in the Orange, Congaree, and Georgeville in order. These relative values indicate that differences existed in that order between the three soils in the number of channels that allow movement of water from the soil surfaces, and may have been to some extent correlated with porosity of soil.

Wilting Percentage—The results of the determinations of the wilting percentages are presented in Table 3. It is evident that the wilting percentage values are higher at the surface than at 2.0 to 3.5 inches. Duplicate determinations of the organic matter in the soil horizons show that the surface soils contained a higher percentage than other horizons and that the amount decreased with increasing depth. The presence of the larger amounts of organic matter in the surface soils may have accounted for at least part of the increased values at the surface. Since the amounts of the smaller soil fractions (Table 1) were approximately the same in the two upper horizons, it does not appear that the wilting percentage values were appreciably affected thereby.

Higher wilting percentage values in other horizons were generally correlated with proportionately higher amounts of the smaller soil fractions. The high wilting percentages of the B horizons of the Georgeville and Orange profiles are rather striking and undoubt-

TABLE 3. Mean wilting percentages, with the standard error of each mean, for the Congaree, Georgeville, and Orange soils at depths indicated.

	Congaree	Georgeville	Orange
Surface (0-1.5 inches)[1]	7.68±0.23	6.16±0.31	4.31±0.21
2-3.5 inches[2]	5.34±0.63	5.54±0.43	3.03±0.08
10-11.5 inches[2]	2.24±0.33	20.51±1.12	10.41±0.51
23-24.5 inches[2]	4.58±0.61	22.85±1.27	....

[1] 20 determinations on each area for every mean.
[2] 9 determinations on each area for every mean.

edly were important in regard to amount of water available to vegetation that the soils were supporting.

Available Soil Moisture—The determinations of total soil moisture which were made at each site during the spring and summer of 1936 were averaged by means of the summation method. For example, the moisture contents of three surface samples from the Congaree soil taken on a certain date were added together. Then the oven-dry weights of the soil samples were added and the percentage of moisture on an oven-dry weight basis was determined by using the sums obtained. Available soil moisture was then obtained by use of the wilting percentages as given in Table 3. The determinations of the available soil moisture are presented in tabular form in Table 4 and in graphic form in Figure 1 along with precipitation data for that period of time. Data on precipitation are presented because it is a determinant of soil moisture. These data indicate the relative moisture conditions of the three sites.

TABLE 4. Available soil moisture on an oven-dry weight basis in the Congaree, Georgeville, and Orange profiles at various dates throughout the spring and summer of 1936.

Depth in Inches	DATE						
	May 5	May 17	May 25	June 15	June 26	July 23	Aug. 6
CONGAREE							
0- 1	13.55	9.98	7.64	17.42	23.20	22.16	13.82
2- 5	14.40	11.49	11.52	12.72	16.67	15.25	13.25
10-13	17.34	14.92	12.24	9.53	20.32	19.17	16.43
23-25	.....	13.89	11.68	20.02	9.61	18.72	14.28
GEORGEVILLE							
0- 1	10.19	7.73	8.99	19.94	9.48	4.82	23.47
2- 5	9.90	6.33	6.42	19.52	10.80	3.46	19.01
10-13	14.22	4.84	4.84	16.94	1.40	16.56	11.54
23-25	.....	4.47	3.85	12.94	4.17	9.80	14.96
ORANGE							
0- 1	8.51	0.96	1.97	29.33	29.81	30.07	25.69
2- 5	8.18	2.58	1.95	15.14	19.50	16.33	13.91
10-13	11.76	6.84	1.02	12.00	18.02	10.42	8.57

Throughout the dry period during May and early June up until the heavy rains occurred, the available moisture content of the soils at all depths gradually decreased until it became quite low in some horizons. There was always some available moisture in all horizons. A comparison of the conditions in the three soils during this period shows that the Orange soil contained the smallest amount of available moisture and the Congaree soil the largest amount. After a few
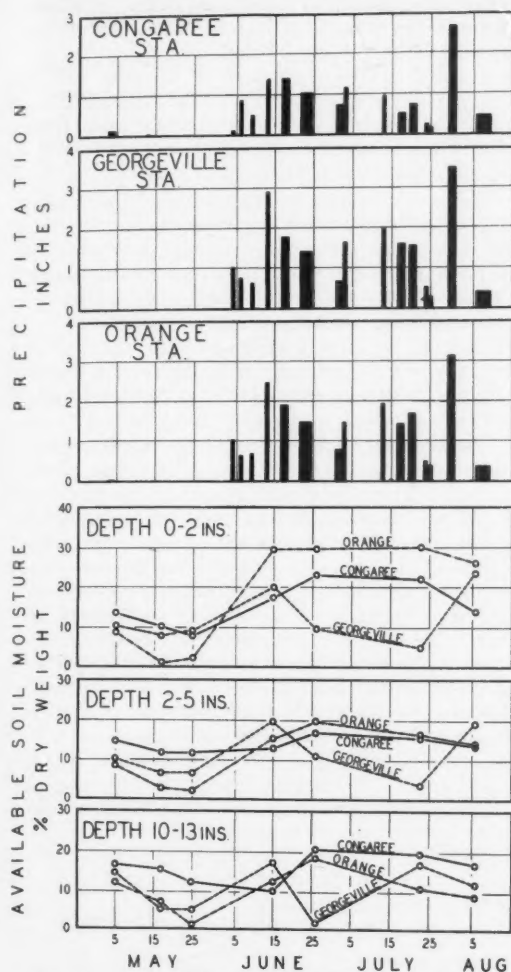
FIG. 1. *Precipitation* records by individual storms from May 1, 1936 through August 15, 1936 at Congaree, Georgeville, and Orange stations. Inches of precipitation are indicated by vertical extent of blocks; duration by lateral extent.

Available Soil Moisture obtained as difference between periodic determination of total soil moisture and the wilting percentage of Congaree, Georgeville, and Orange soils at depths indicated.

inches of rainfall the two upper horizons of the Orange profile became very moist because the water was unable to percolate rapidly down into or through the relatively impervious B horizons.

Apparently the available moisture content in the Congaree horizons also became rather high after a rain of a few inches had fallen, particularly if the area became inundated after a heavy storm. Since the water was able to percolate through the surface horizons more readily than in those of the Orange, the available moisture content at lower depths usually became higher than at the same depths in the Orange. This situation obtained at a depth of 10 to 13 inches

from June 25 to the end of the period of study. The amount of available moisture throughout the Georgeville profile, during the same period, was generally less than in the other two profiles unless exceptionally heavy rains occurred. Since water was able to percolate through the surface horizons at a much more rapid rate in the Georgeville than in the other two soils, medium amounts of rainfall generally penetrated to lower horizons of the soil.

During periods of normal amounts of rainfall, then, the surface horizons of the Orange profile contained more available moisture than the other two soils and the Georgeville contained the least. When conditions began to become dry in late spring and the total amounts of available moisture in each soil became smaller, the relative amounts were changed and the Congaree soil had more available moisture than the other two soils and the Orange had the least.

OTHER SOIL CONDITIONS

Air Capacity and Volume-weight—In addition to water-holding capacity values for the three soils, Table 2 shows the results of determinations of air capacity percentage on a volume basis and of volume weights. In each horizon all differences between the mean air capacities of the three soils are significant except between the Congaree and Georgeville at the surface and at 10 to 12 inches, and between the Orange and Georgeville at the surface and at 2 to 4 inches.

The air capacities of the two upper horizons were greatest in the Orange, least in the Congaree, and intermediate in the Georgeville. Since the average percolation rates of the three soils at the surface fell in a different order, the air capacities therefore were not important in that connection. The air capacities of the lower two horizons of the Congaree and Georgeville soils were all of about the same value except that the Congaree at a depth of 23 to 25 inches was about 2 percent higher. At this depth in the Congaree soil there was a high percentage of sand and so it might well have been expected to be higher. At 10 to 12 inches in the Orange there was only a small air capacity. This is another indication of the extremely compact nature of the Orange soil at that depth. The highest of all volume-weight values was also at the same horizon and thus is further confirmation of its compactness.

Porosity—The water retained by a soil occupies the soil pore space. This water, therefore, may be used as a basis to measure the soil pore space provided the soil is saturated. Therefore the measurements of the water-holding capacity on a volume basis (Table 2) give measures of the porosity of the soil except for the air capacity of the soil. Combining the two values then gives a value for the porosity. Values for each depth in the three soils appear in Table 5. The two surface horizons were most porous in the Congaree and least porous in the Orange soil. It is also apparent that the porosity in each soil decreased with depth except at 23 to 25 inches, and that the Orange

TABLE 5. Percentage of porosity of Congaree, George-
ville, and Orange soils as indicated by the sum of per-
centages of air and water-holding capacities on volume
bases.

Depth	Congaree	Georgeville	Orange
Surface..........	54.90	53.29	47.96
2- 4 inches......	49.33	46.72	43.22
10-12 inches......	33.81	44.87	28.57
23-25 inches......	37.15	45.82	.....

soil at 10 to 12 inches was least porous of all horizons
of the three soils.

Air Space and Soil Atmosphere Analysis—The data
obtained from the studies of soil air space and soil
atmosphere during April and October, 1935 appear
in Table 6. Based on the two sets of determinations
which were made in duplicate, several facts pertain-
ing to all three soils are evident: namely, that the
carbon dioxide content of the soil air increased with
the depth below the surface while the oxygen content
decreased slightly with depth; that the percentage of
oxygen was high, never falling below 20 percent at
any depth; and that the conditions in each of the
soils were different at the two different seasons.

TABLE 6. Mean percentages of carbon dioxide and
oxygen in the soil air and of the soil air space by vol-
ume, and moisture content of the soil on a dry-weight
basis at the time of the determinations, April 1935 and
October 1935, in Congaree, Georgeville, and Orange soils.

	Congaree		Georgeville		Orange	
	April	October	April	October	April	October
SURFACE						
Carbon dioxide...	0.07	0.18	0.22	0.30	0.67	0.15
Oxygen..........	20.74	20.81	20.44	20.79	20.56	20.74
Air space........	29.20	33.48	29.62	51.23	12.05	41.77
Moisture content.	23.81	25.52	33.59	13.91	31.81	14.80
8 INCHES						
Carbon dioxide...	0.45	0.20	0.44	0.24	1.50	0.29
Oxygen..........	20.70	20.78	20.56	20.76	20.15	20.67
Air space........	19.61	29.61	22.86	39.75	10.04	27.59
Moisture content.	25.64	15.75	28.21	23.93	21.63	14.94
12 INCHES						
Carbon dioxide...	0.86	0.29	0.61	0.37	1.47	0.66
Oxygen..........	20.21	20.78	20.58	20.64	20.12	20.70
Air space........	22.43	27.41	24.56	39.09	25.39	34.65
Moisture content.	24.70	14.88	34.43	31.50	18.76	14.53
24 INCHES						
Carbon dioxide...	1.13	0.80	0.74	1.04	1.56	1.13
Oxygen..........	20.41	20.65	20.65	20.44	20.08	20.51
Air space........	22.01	46.50	20.75	32.16	24.16	35.98
Moisture content.	19.69	11.57	39.22	34.71	.....	20.76

Comparison of the carbon dioxide contents of the
three soils in April at the various depths reveals that
with the exception of the surface soils the content
was greatest in the Orange and least in the George-
ville. This was probably due to the relative air spaces
in the soils. Since the speed of diffusion of carbon
dioxide produced at a constant rate has quite an in-
fluence upon the concentration of this gas (Russell,

1932) and diffusion is directly related to free pore
space or air space (Buckingham, 1904; Smith and
Brown, 1933), it appears that carbon dioxide con-
tent in soil is inversely related to air space through
influence of air space on rate of diffusion of carbon
dioxide. It has been demonstrated by Letts and Blake
(1900) that carbon dioxide in soil air varies directly
with porosity (free pore space) of a soil.

It must be recognized that carbon dioxide content
of soil air is dependent on a production factor as
well as on a diffusion factor. It has been shown by
Boussingault and Lewy (1853), Stoklassa (1926),
Fischer (1927), and others that the carbon dioxide
content depends on factors that increase the rate of
production. In this study no attempt was made to
determine the factors influencing the rate of produc-
tion, or to determine whether the rates were different
in the three soils.

A comparison of the carbon dioxide contents of the
three soils in October reveals that the carbon dioxide
content was inversely proportional to the air space
in the soils as compared to the April values. The
carbon dioxide content may not appear to have been
correlated at lower depths, but when the air spaces
in the horizons above (through which the gases must
diffuse to escape into the air) are considered, the
relation holds. For example, even though the air
space in the Georgeville and Orange soils at a depth
of 12 inches was approximately the same, the carbon
dioxide contents were radically different. However,
in the horizons above, the air spaces were quite dif-
ferent and thus influenced the carbon dioxide content
below them. As carbon dioxide content was not
inversely proportional to the air space when the
differences existing between the Georgeville and Con-
garee soils were considered, it is supposed that a
shift was brought about by differences in the amount
of gas produced in the soils.

From data obtained from studies of soil air space
and soil atmosphere it can be concluded that, all
other factors being approximately equal, carbon diox-
ide content in all three soils varied inversely with
air space, and therefore carbon dioxide must have
varied to a certain extent directly with water con-
tent of the soil. It can also be concluded that under
ordinary conditions oxygen content did not reach a
low value and that carbon dioxide content although
increasing considerably with depth did not reach a
concentration much above 1.5 percent at any depth
down to two feet.

Root Distribution—Tabulation of the number of
roots in the soil transects from the three experimental
areas brings out differences in the number per square
foot. The average number of roots of all size classes
per square foot on the basis of the three 6-foot tran-
sects from each area are given in Table 7. The data
are analyzed for 3-inch depths down to 18 inches.
There were the most roots in the Congaree soil and
the least in the Georgeville soil with two exceptions;
as there were the greatest number at 0 to 3 inches
and the least at 15 to 18 inches in the Orange soil.

TABLE 7. Number of roots per square foot at depths indicated in Congaree, Georgeville, and Orange soils, as determined from soil transects.

Depth in Inches	Congaree	Georgeville	Orange
0-3	242.0	230.9	250.4
3-6	132.7	96.2	103.3
6-9	98.2	58.0	84.0
9-12	74.0	51.1	64.9
12-15	57.6	36.0	37.8
15-18	66.7	33.3	26.7

RESULTS OF STUDY OF SEEDLINGS

SEEDLING ESTABLISHMENT AND SURVIVAL IN SEED BEDS

The first indication of a difference in reactions of seedlings to their edaphic environments was obtained from a study of seedling establishment and survival. Seedlings that grew from seeds planted in plots in the autumn of 1934 were considered to have established themselves if, on June 1, 1935, they appeared to be in good growing condition. The total number of seeds of each species planted in each experimental area, the percentage of seedlings that had become established, and the percentage of established seedlings that had survived until October 1, 1935 and May 20, 1936 appear in Table 8. The values given for May 20, 1936 include the live specimens that were dug for study during March and April, 1936. Accurate data concerning establishment and survival of dogwood and red cedar seedlings was not obtained because of unevenly delayed germination of their seeds.

Establishment of seedlings of each species is, of course, partly due to degree of viability of seeds.

TABLE 8. Number of seeds of each species planted; percentage of seedlings established by June 1, 1935; and percentage of established seedlings surviving on October 1, 1935 and May 20, 1936[1] in the seed beds of each experimental area.

Species	Total seeds planted on each area autumn, 1934	Congaree Soil 6/1/35	Congaree Soil 10/1/35	Congaree Soil 5/20/36	Georgeville Soil 6/1/35	Georgeville Soil 10/1/35	Georgeville Soil 5/20/36	Orange Soil 6/1/35	Orange Soil 10/1/35	Orange Soil 5/20/36
White oak	70	74	96	64	80	98	91	39	100	100
Post oak	100	62	82	35	58	95	84	35	97	91
Blackjack oak	80	12	80	10	16	100	85	9	100	86
Black oak	80	14	73	45	15	100	83	9	100	100
Scarlet oak	80	9	86	14	5	100	75	4	33	33
Northern red oak	80	19	100	80	16	100	77	25	75	75
Loblolly pine	280[2]	5	79	0	8	86	32	5	87	33
Red cedar	320	0	0	0	1	100	100	0	3[3]	5[3]
Yellow poplar	200	3	0	0	5	100	30	2	0	0
Dogwood	180	6	6[3]	8[3]	3	1[3]	16[3]	0	6[3]	6[3]
Red gum	400	12	76	0	28	68	17	25	80	5
Sourwood	1000	0	0	0	11	41	0	0	0	0

(header note over data columns: Percentage of seedlings established by June 1, 1935 and percentage of established seedlings that survived until October 1, 1935 and May 20, 1936.)

[1] Includes live specimens dug in March and April, 1936.
[2] Figures in *Italics* are approximations.
[3] Total percentages established by each date.

The seeds of each species were well mixed before they were planted in the seed plots and, therefore, the factor of viability should not affect establishment in one area more than in another, unless conditions that influence germination through viability changes are different in the soil environments in which they were planted.

It has been shown by Korstian (1927) that white oak and red oak acorns have a marked decrease in viability upon decrease of their moisture content below certain levels. This factor probably had no significant effect in the present study in any of the three soils, because, from the time of seeding until germination was completed, the soils were very moist and the seeds were sufficiently covered to prevent appreciable drying out. Establishment of seedlings, however, was probably affected by excessive moisture in soil during rainy periods up until May, 1935.

The small percentage of seedlings established in the Orange seed plots as compared with the other two pairs of plots on Congaree and Georgeville soils, was probably due to a combination of two factors. Roots of many seedlings in the Orange soil were found to be infected with an abundant growth of damping-off fungus (a species of Rhizoctonia, probably *R. solani* Kühn). Many young seedlings were killed by the fungus in the early spring of 1935. Some infection by Rhizoctonia was found in the other two soils, but fewer seedlings were affected to the extent that they were killed by this fungus.

The other factor that might have aided in reducing seedling establishment was the higher carbon dioxide content of the Orange soil horizons in comparison with the other two soils. This factor has been found to be important by earlier investigators. Free (1917) found that buckwheat plants died because of a high content of carbon dioxide in soil air. Hole (1918) found that injury to plants in poorly aerated soils was due to an excess of carbon dioxide. Determinations of carbon dioxide content of soil air at the time of poor aeration during wet periods were attempted, but because of the extremely wet condition of soil, samples of air could not be obtained from the soil for analyses.

As is shown in Table 6, the carbon dioxide content of soil air was largest in the Orange soil and increased with moisture content of soils. Therefore it would be expected that carbon dioxide content would have been high in the Orange soil air at the time when the surface horizons were essentially saturated with water. The entire area of the Congaree soil was completely inundated at least once between October 1, 1935 and the following spring. The resultant high moisture content and general effect of the new layer of alluvium on the soil brought about conditions that induced a large amount of rotting of roots and caused the death of several individual seedlings. There was no way to prove conclusively that root rot preceded death of seedlings; however, the existence of all stages of rotting from small amounts in live individuals to large amounts in dead ones, indicated that this was the case.

Another factor that decreased the percentage of surviving seedlings was the frost-heaving of certain seedlings during the severe weather of the winter of 1935-36. This was especially true for the seedlings of the smaller sized species, such as red gum and sourwood, while species with deeper root penetration were little affected.

Survival was high in the oaks growing in the Georgeville and Orange soils. Apparently after the seedlings had matured sufficiently to resist damping off, they were generally able to maintain themselves in the two soils.

SEEDLING DEVELOPMENT

A study of the development of four of the species from which it had been hoped to obtain data was necessarily discontinued. The data presented in Table 8 show that an insufficient number of sourwood and yellow poplar seedlings was present in the spring of 1936 to allow any comparison of the two species grown in the three soils, and so when naturally seeded one-year specimens could not be located, no further attention was given these two species in this study. Available material of dogwood and scarlet oak proved inadequate and they too were dropped from the study.

Data were obtained for the 10 remaining species, a total of 372 seedlings being excavated. Many of these seedlings had been injured and were not used in the measurements and data presented. Injuries were apparently due mostly to rotting as a result of poor aeration and fungous attacks, and heaving by winter frosts. Injuries caused by the latter factor were confined to the shallow-rooted species of loblolly pine, red cedar, and red gum. Injury as a result of poor aeration was observed on all species but was apparently absent in the Georgeville area. Fungous attacks were observed to have caused injury on all species and in all three areas, injury being least severe in the Georgeville area.

Except for blackjack oak, northern red oak, and red cedar, the data obtained from uninjured specimens were treated statistically. Out of the 84 differences between means that are significant only 22 have a probability greater than 0.01. Thus differences in growth of seedlings were probably a result of differences in environments in which the seedlings grew. In the data concerning plant development, linear measurements are given in inches and weights in grams.

White Oak

The development of both 1- and 2-year-old white oak seedlings was studied. Mean measurements of uninjured 1-year-old seedlings, difference between means, and significance of differences are presented in Table 9. From the data it is readily seen that, except for maximum depth of root penetration and weight of top, all mean measurements of specimens from the Congaree area are smallest and from the Orange area are largest. It is also evident that most of the differences between means are statistically significant.

TABLE 9. Mean measurements of 1-year-old white oak seedlings[1] from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree........	0.468 ± 0.018[3]	0.164 ± 0.004	0.305 ± 0.022
Georgeville......	0.808 ± 0.074	0.213 ± 0.018	0.595 ± 0.060
Orange..........	1.094 ± 0.107	0.211 ± 0.030	0.882 ± 0.078
Difference between means			
Congaree and Georgeville....	0.340	0.049	0.290
Georgeville and Orange........	0.286	0.002	0.287
Orange and Congaree......	0.626	0.047	0.577
Significance of differences			
Congaree and Georgeville....	4.46**	2.69*	4.53**
Georgeville and Orange........	2.20	0.09	2.92*
Orange and Congaree......	5.80**	1.57	7.12**

Area	Relative Weight of Root[2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree........	64.80 ± 1.83	12.6 ± 0.27	22.8 ± 1.38
Georgeville......	73.48 ± 1.11	12.4 ± 0.71	46.2 ± 5.68
Orange..........	81.01 ± 1.19	11.1 ± 0.47	51.5 ± 10.79
Difference between means			
Congaree and Georgeville....	8.68	0.2	23.4
Georgeville and Orange........	7.53	1.3	5.3
Orange and Congaree......	16.21	1.5	28.7
Significance of differences			
Congaree and Georgeville....	4.06**	0.26	4.01**
Georgeville and Orange........	4.65**	1.53	0.42
Orange and Congaree......	7.44**	2.73*	2.64*

[1] 6 specimens from Congaree, 6 from Georgeville, and 5 from Orange area.
[2] Expressed as percentage of total plant weight.
[3] Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

The data for uninjured, 2-year-old seedlings (Table 10) were obtained from those remaining in seed plots and from naturally seeded specimens. The average measurements are larger, as is to be expected, and fall in the same order of magnitude as those of 1-year-old seedlings. All differences between means, except for two, are statistically significant. The greater number of 2-year-old specimens enabled a larger number of statistically significant differences to be established.

Drawings of typical root systems of 1-year-old white oak seedlings are shown in Figure 2. There were very few roots in the A_1 horizons of all three

TABLE 10. Mean measurements of 2-year-old white oak seedlings[1] from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree........	0.7282 ± 0.0554[3]	0.2449 ± 0.0190	0.4833 ± 0.0409
Georgeville.......	0.9878 ± 0.0739	0.2860 ± 0.0214	0.7018 ± 0.0545
Orange..........	1.8191 ± 0.1276	0.3892 ± 0.0321	1.4298 ± 0.1030
Difference between means			
Congaree and Georgeville....	0.2596	0.0411	0.2185
Georgeville and Orange........	0.8313	0.1032	0.7280
Orange and Congaree......	1.0909	0.1443	0.9465
Significance of differences			
Congaree and Georgeville....	2.88**	1.48	3.28**
Georgeville and Orange........	5.86**	2.67*	6.31**
Orange and Congaree......	8.29**	3.93**	9.00**

Area	Relative Weight of Root[2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree........	66.19 ± 1.56	11.1 ± 0.77	34.6 ± 1.99
Georgeville.......	70.89 ± 0.85	10.9 ± 0.44	48.8 ± 2.80
Orange..........	78.52 ± 0.92	13.6 ± 0.84	69.4 ± 6.30
Difference between means			
Congaree and Georgeville....	4.70	0.2	14.2
Georgeville and Orange........	7.63	2.7	20.6
Orange and Congaree......	12.33	2.5	34.8
Significance of differences			
Congaree and Georgeville....	2.78*	0.24	4.19**
Georgeville and Orange........	6.25**	2.86**	2.98**
Orange and Congaree......	7.25**	2.31*	5.27**

[1] 8 specimens from Congaree, 16 from Georgeville, and 10 from Orange area.
[2] Expressed as percentage of total plant weight.
[3] Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

soils and in the B_1 horizon of the Orange soil. The root system shown in Figure 2A had more secondary roots in the A_1 horizon than the average seedling growing on Orange soil, but was otherwise representative.

Attention should be called to the initial root habit of white oak seedlings. It is apparent in Figure 2 that the slanting main radicle, which is characteristic of the initial root habit, was not essentially changed by the soil type in which it grew.

Post Oak

The relative measurements (Table 11) of 1-year-old post oak seedlings from the three areas fall mostly

FIG. 2. Typical root systems of 1-year-old white oak seedlings: A, from Orange soil; B, from Georgeville soil; and C, from Congaree soil.

in the same order as those of white oak. The growth of 1-year-old post oak seedlings as indicated by the measurements presented was less than that of white oak seedlings in the same areas.

Drawings of typical root systems of 1-year-old post oak seedlings that had grown in the three experimental areas appear in Figure 3. There were noticeably fewer secondary roots on these specimens than were found on the white oak seedlings from the same corresponding areas. This was also shown by measurements of the secondary roots. Frequently in the seedlings from the Orange soil there were very few
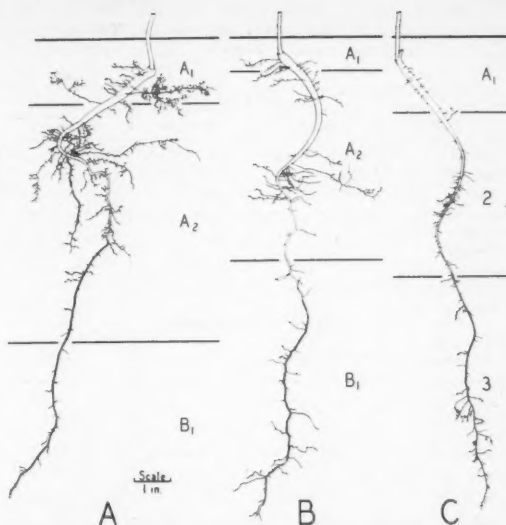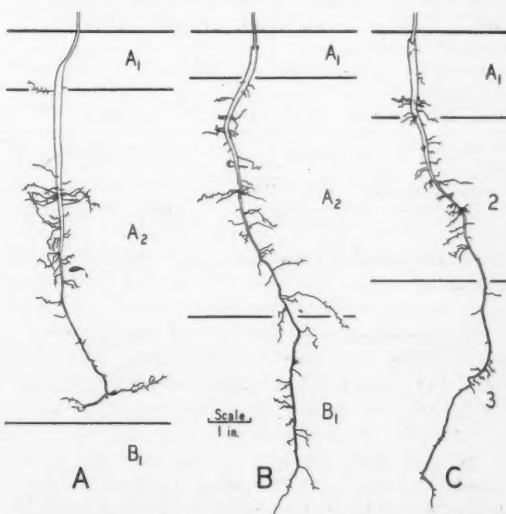

FIG. 3. Typical root systems of 1-year-old post oak seedlings: A, from Orange soil; B, from Georgeville soil; and C, from Congaree soil.

TABLE 11. Mean measurements of 1-year-old post oak seedlings from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree.........	0.209±0.008	0.061±0.004	0.148±0.005
Georgeville.......	0.305±0.046	0.060±0.006	0.245±0.040
Orange...........	0.632±0.054	0.093±0.C17	0.539±0.042
Difference between means			
Congaree and Georgeville....	0.096	0.001	0.097
Georgeville and Orange........	0.327	0.033	0.294
Orange and Congaree......	0.423	0.032	0.391
Significance of differences			
Congaree and Georgeville....	2.04	0.16	2.43*
Georgeville and Orange........	4.61**	1.78	5.04**
Orange and Congaree......	7.89**	1.78	5.70**

Area	Relative Weight of Root [2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree.........	70.99±1.31	11.3±1.24	13.5±1.14
Georgeville.......	79.44±1.00	9.4±0.32	24.2±1.68
Orange...........	85.13±0.44	10.5±1.60	22.8±1.36
Difference between means			
Congaree and Georgeville....	8.45	1.9	10.7
Georgeville and Orange........	5.69	1.1	1.4
Orange and Congaree......	14.14	0.8	9.3
Significance of differences			
Congaree and Georgeville....	5.12**	2.29*	3.66**
Georgeville and Orange........	5.22**	1.08	0.49
Orange and Congaree......	10.25**	0.66	6.31**

[1] 6 specimens from Congaree, 8 from Georgeville, and 4 from Orange area.
[2] Expressed as percentage of total plant weight.
[3] Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

secondary roots on that part of the main radicle that was in the upper few inches of the soil. This type of development is displayed by seedling A in Figure 3. In the Orange soil this type of development appeared to be as common as other types. Initial root habit was maintained by post oak seedlings in all three soils.

Black Oak

The data from 1-year-old black oak seedlings are presented in Table 12. Drawings of root systems of 1-year-old seedlings typical of their development in each area are shown in Figure 4. All but two of the mean measurements are largest in the Orange and smallest in the Congaree soil. The variation in seedlings from the Orange area was rather large and since only three seedlings were available, in many cases significant differences between their mean measurements and the mean measurements of seedlings from the other soils were not established. It should be noted that secondary root development seems to have been retarded in the Orange area as root growth, as expressed on a dry weight basis, was greatest in the Orange area and therefore indicates a tendency toward a greater development of secondary roots.

General observations indicated that seedlings in the Orange and Congaree soils were not as vigorous as those in the Georgeville soil.

TABLE 12. Mean measurements of 1-year-old black oak seedlings[1] from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree.........	0.285±0.009[3]	0.121±0.005	0.164±0.004
Georgeville.......	0.651±0.013	0.178±0.009	0.473±0.035
Orange...........	0.995±0.279	0.221±0.060	0.775±0.217
Difference between means			
Congaree and Georgeville....	0.366	0.057	0.309
Georgeville and Orange........	0.344	0.043	0.302
Orange and Congaree......	0.710	0.100	0.611
Significance of differences			
Congaree and Georgeville....	24.40**	5.70**	8.88**
Georgeville and Orange........	1.38	0.80	1.54
Orange and Congaree......	2.85*	1.85	3.17*

Area	Relative Weight of Root [2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree.........	57.48±0.45	12.1±0.07	31.4± 3.43
Georgeville.......	72.48±1.33	10.7±0.49	61.5± 3.15
Orange...........	77.86±0.09	12.9±2.32	49.7±12.38
Difference between means			
Congaree and Georgeville....	15.00	1.4	30.1
Georgeville and Orange........	5.38	2.2	11.8
Orange and Congaree......	20.38	0.8	18.3
Significance of differences			
Congaree and Georgeville....	9.38**	2.80*	7.08**
Georgeville and Orange........	4.04**	1.69	1.03
Orange and Congaree......	22.92**	0.66	1.60

[1] 4 specimens from Congaree, 6 from Georgeville, and 3 from Orange area.
[2] Expressed as percentage of total plant weight.
[3] Standard error.
*Significant at 5 percent level.
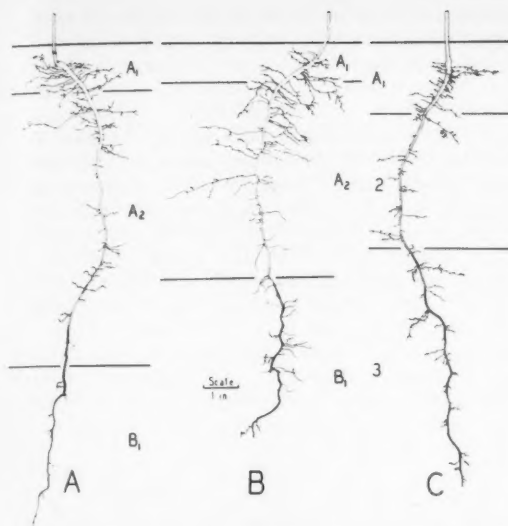**Significant at 1 percent level.

FIG. 4. Typical root systems of 1-year-old black oak seedlings: A, from Orange soil; B, from Georgeville soil; and C, from Congaree soil.

Loblolly Pine

All loblolly pine seedlings in the Congaree seed plots were killed by rotting before they were excavated and studied. Nine naturally seeded, uninjured, 1-year-old specimens were obtained later. Also, some naturally seeded specimens were found in the other two areas and were included in the number from which data were obtained.

Table 13 presents the data obtained for 1-year-old loblolly pine seedlings from the three areas. The fact that mean measurements of seedlings from the Orange area are much larger than from the other areas may have been associated with the presence of mycorrhiza on the roots of the seedlings from that area. It should be noted that all but two of the differences between the means of measurements are statistically significant.

Drawings of one typical root system from each area are given in Figure 5. The meager root systems
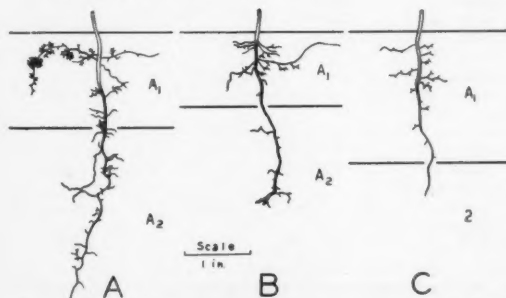

FIG. 5. Typical root systems of 1-year-old loblolly pine seedlings: A, from Orange soil; B, from Georgeville soil; and C, from Congaree soil.

TABLE 13. Mean measurements of 1-year-old loblolly pine seedlings[1] from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree........	0.0391 ± 0.0047[3]	0.0266 ± 0.0032	0.0125 ± 0.0020
Georgeville.......	0.0397 ± 0.0015	0.0242 ± 0.0013	0.0155 ± 0.0005
Orange...........	0.1161 ± 0.0216	0.0530 ± 0.0086	0.0631 ± 0.0130
Difference between means			
Congaree and Georgeville....	0.0006	0.0024	0.0030
Georgeville and Orange........	0.0764	0.0288	0.0476
Orange and Congaree......	0.0770	0.0264	0.0506
Significance of differences			
Congaree and Georgeville....	0.12	0.71	1.43
Georgeville and Orange........	3.54**	3.31**	3.65**
Orange and Congaree......	3.47**	2.90*	3.83**

Area	Relative Weight of Root[2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree.........	31.49 ± 2.53	2.5 ± 0.2	3.7 ± 0.6
Georgeville.......	39.26 ± 1.30	2.4 ± 0.3	5.9 ± 0.3
Orange...........	53.52 ± 1.16	3.1 ± 0.3	19.5 ± 4.0
Difference between means			
Congaree and Georgeville....	7.77	0.1	2.2
Georgeville and Orange........	14.26	0.7	13.6
Orange and Congaree......	22.03	0.6	15.8
Significance of Differences			
Congaree and Georgeville....	2.45*	0.29	2.06
Georgeville and Orange........	8.19**	1.84	3.43**
Orange and Congaree......	7.92**	1.76	3.86**

[1] 9 specimens from Congaree, 6 from Georgeville, and 6 from Orange area.
[2] Expressed as percentage of total plant weight.
[3] Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

possessed by the seedlings from the Congaree and Georgeville areas are evident.

Blackjack Oak

Very few 1-year-old blackjack oak seedlings were available for study (Table 8) and only seven uninjured specimens were obtained. The average measurements are presented in Table 14. No statistical treatment was attempted in view of the small number of seedlings. No definite conclusions can be drawn but it appears that development was best in those seedlings from the Orange area. It should be pointed out that depth of root penetration was apparently least in the Orange area.

TABLE 14. Mean measurements of a number of 1-year-old blackjack oak, northern red oak, red cedar, and red gum seedlings excavated from Congaree, Georgeville, and Orange areas.

Area	Number of Specimens	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams	Relative Weight of Root[1]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
			BLACKJACK OAK				
Congaree........	1	0.242	0.079	0.163	67.35	12.2	25.3
Georgeville......	4	0.190	0.062	0.128	67.37	8.4	24.6
Orange.........	2	0.296	0.076	C.220	74.37	7.1	28.8
			NORTHERN RED OAK				
Congaree........	3	0.468	0.164	0.303	64.90	10.8	41.7
Georgeville......	2	0.566	0.174	0.391	69.21	8.7	77.8
Orange.........	1	1.318	0.434	0.884	67.07	8.5	83.4
			RED CEDAR				
Georgeville......	2	0.0102	0.0049	0.0053	51.96	1.4	2.0
Orange.........	3	0.0197	0.0071	0.0126	63.91	2.2	5.8
			RED GUM				
Georgeville......	5	0.0189	0.0132	0.0057	30.16	1.5	2.1
Orange.........	3	0.0321	0.0172	C.0149	46.45	3.8	4.5

[1]Expressed as percentage of total plant weight.

Northern Red Oak

There were seven uninjured, 1-year-old northern red oak seedlings available for study. The measurements made (Table 14) indicate that the development of northern red oak seedlings in the three soils was best in the Orange soil and poorest in the Congaree soil.

Red Cedar

Data in regard to the development of red cedar seedlings in the Congaree area were not obtainable, as no seedlings were established in the seed plots (Table 8) and no naturally seeded, 1-year-old specimens could be located. The average measurements of uninjured specimens from the other two areas are presented in Table 14. The data, on the basis of all sets of measurements, indicate that red cedar seedlings attained a better growth in the Orange area than in the Georgeville area.

Red Gum

Specimens of 1-year-old red gum could not be obtained from the Congaree area and only those in the seed plots (Table 8) could be located in the other two areas. Injury by heaving was especially severe in the case of these seedlings, the secondary roots having been stripped off and the root of the main axis of some having been broken. Five uninjured specimens were obtained from the Georgeville plots, and three from the Orange. Their mean measurements are presented in Table 14.

All differences between means, except those of relative weight of root, are not statistically significant. These measurements indicate that there was a better growth on 1-year-old red gum seedlings in the Orange area than in the Georgeville. The distribution of the roots was apparently due only to the magnitude of the development of each individual root system and was little affected by the soil type in which they grew.

Red Maple

It was possible to obtain a number of naturally-seeded, 1- and 2-year-old red maple seedlings from the Congaree and Georgeville areas, although none could be located in the Orange area. When the measurements were averaged for each area and the results treated statistically (Table 15), it was found that all of the differences between the means, except for that of the relative weight of root of 2-year-old seedlings, are statistically significant. It is evident that in all probability there was a correlation between development of 1- and 2-year-old red maple seedlings and the environment in which they grew. The Georgeville area was therefore apparently more favorable to the growth of red maple during its first 2 years of growth. Root habit did not appear to be affected by the edaphic environment. All of the seedlings had developed practically no main radicle but had a good development of secondary roots.

TABLE 15. Mean measurements ot 1- and 2-year-old red maple seedlings[1] from the Congaree and Georgeville areas; differences between means; and significance of differences.

	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Area		1 Year Old	
Congaree........	0.0222 ± 0.0027[3]	0.0120 ± 0.0012	0.0102 ± 0.0016
Georgeville......	0.0471 ± 0.0017	0.0229 ± 0.0017	0.0242 ± 0.0005
Difference between means........	0.0249	0.0109	0.0140
Significance of differences.....	7.78**	5.19**	8.75**
Area		2 Year Old	
Congaree........	0.0473 ± 0.0040	0.0207 ± 0.0013	0.0266 ± 0.0029
Georgeville......	0.0845 ± 0.0010	0.0367 ± 0.0009	0.0478 ± 0.0010
Difference between means........	0.0372	0.0160	0.0212
Significance of differences.....	8.94**	9.25**	6.84**

	Relative Weight of Root[2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Area		1 Year Old	
Congaree........	44.67 ± 2.15	1.9 ± 0.12	6.0 ± 0.9
Georgeville......	51.64 ± 2.01	2.2 ± 0.07	13.2 ± 0.7
Difference between means........	6.97	0.3	7.2
Significance of differences.....	2.37*	2.17*	6.15**
Area		2 Year Old	
Congaree........	55.28 ± 1.13	1.9 ± 0.15	14.2 ± 1.13
Georgeville......	56.60 ± 0.75	2.3 ± 0.05	25.5 ± 1.11
Difference between means........	1.32	0.4	11.3
Significance of differences.....	0.65	2.52*	6.28**

[1]1-year old specimens, 9 from Congaree and 10 from Georgeville; 2-year old specimens, 10 from Congaree and 9 from Georgeville.
[2]Expressed as percentage of total plant weight.
[3]Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

One of the interesting relations which is apparent when the data are examined is that the relative weight of root increased during the second year.

Downy Viburnum

Downy viburnum grew naturally on all three experimental areas, but was most abundant in the Congaree area. The development of both 1- and 2-year-old seedlings from the three areas was studied. The mean measurements that were obtained from the 1-year-old seedlings, the difference between means, and significance of differences are presented in Table 16. The data from the 2-year-old seedlings are given in Table 17.

TABLE 16. Mean measurements of 1-year-old downy viburnum seedlings[1] from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree.........	0.0319±0.0008[3]	0.0141±0.0006	0.0178±0.0008
Georgeville.......	0.0358±0.0007	0.0143±0.0007	0.0215±0.0007
Orange...........	0.0401±0.0033	0.0142±0.0016	0.0259±0.0019
Difference between means			
Congaree and Georgeville....	0.0039	0.0002	0.0037
Georgeville and Orange........	0.0043	0.0001	0.0044
Orange and Congaree......	0.0082	0.0001	0.0081
Significance of differences			
Congaree and Georgeville....	3.51**	......	3.56**
Georgeville and Orange........	1.26	......	2.20*
Orange and Congaree......	2.41*	......	3.86**

Area	Relative Weight of Root[2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree.........	55.58±1.82	2.3±0.7	9.4±0.46
Georgeville.......	60.11±1.61	2.3±0.9	14.0±1.38
Orange...........	64.83±1.51	2.2±0.7	19.4±1.41
Difference between means			
Congaree and Georgeville.......	4.53	....	4.6
Georgeville and Orange........	4.72	0.1	5.4
Orange and Congaree........	9.25	0.1	10.0
Significance of differences			
Congaree and Georgeville....	1.88	....	3.15**
Georgeville and Orange........	2.14*	....	2.74*
Orange and Congaree......	3.92**	....	6.76**

[1]13 specimens from Congaree, 7 from Georgeville, and 10 from Orange area.
[2]Expressed as percentage of total plant weight.
[3]Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

TABLE 17. Mean measurements of 2-year-old downy viburnum seedlings[1] from the Congaree, Georgeville, and Orange areas; differences between means; and significance of differences.

Area	Plant Weight, Grams	Top Weight, Grams	Root Weight, Grams
Congaree.........	0.0608±0.0032[3]	0.0269±0.0017	0.0340±0.0022
Georgeville.......	0.0652±0.0049	0.0288±0.0026	0.0364±0.0026
Orange...........	0.0729±0.0071	0.0302±0.0008	0.0426±0.0043
Difference between means			
Congaree and Georgeville....	0.0044	0.0019	0.0024
Georgeville and Orange........	0.0077	0.0014	0.0062
Orange and Congaree......	0.0121	0.0033	0.0086
Significance of differences			
Congaree and Georgeville....	0.86	0.64	0.74
Georgeville and Orange........	0.92	0.40	1.27
Orange and Congaree......	1.55	1.74	1.79

Area	Relative Weight of Root[2]	Maximum Depth of Root, Inches	Total Length Secondary Roots, Inches
Congaree.........	55.61±1.88	2.5±0.7	22.2±1.68
Georgeville.......	55.92±1.49	2.5±0.9	28.2±1.37
Orange...........	57.63±1.95	2.4±0.8	35.0±2.43
Difference between means			
Congaree and Georgeville....	0.31	....	6.0
Georgeville and Orange........	1.71	0.1	6.8
Orange and Congaree......	2.02	0.1	12.8
Significance of differences			
Congaree and Georgeville....	0.13	....	4.65**
Georgeville and Orange........	0.78	....	2.47*
Orange and Congaree......	0.80	....	5.27**

[1] 14 specimens from Congaree, 9 from Georgeville, and 10 from Orange area.
[2]Expressed as percentage of total plant weight.
[3]Standard error.
*Significant at 5 percent level.
**Significant at 1 percent level.

Difficulty was encountered in determining the point for separation of root from top as there was no pronounced point of basal swelling. For this reason a greater error in sampling was probably introduced. However, it is evident that development of downy viburnum seedlings was somewhat dependent on the environment in which they grew. It should be pointed out that top weight, particularly during the first year, was approximately the same in all three areas. The relative weight of root of 1-year-old seedlings seems to have been different in each experimental area. At the end of 2 years, however, the relative weights of root were approximately the same.

GENERAL DISCUSSION

The differences in development of most of the species studied in the three areas are among the most striking facts that can be shown in regard to the development of seedlings in the three habitats. The data in most cases show that the development, on a dry-weight basis, was greatest in the Orange area and smallest in the Congaree area. Exceptions are mostly in those species of which a very small number of seedlings were available.

Accordingly, with a greater plant development (on a dry weight basis) in a given area than in another, a greater root development might have been expected. This occurred, but perhaps not always in proportion to the increase in plant weight. This is borne out by reference to the values for weight of root relative to plant weight that were obtained for 1- and 2-year-old white oak (Tables 9 and 10). In each area the weight of root relative to plant weight was approximately the same for 1- and 2-year-old seedlings but was not the same in different areas even though the total plant weights may have approached equality, as did the 2-year Congaree seedlings to the 1-year George-ville seedlings. The 2-year-old Georgeville seedlings were almost the same weight as those from the Orange area that were 1 year old, yet there was a considerable difference between values of the weight of root rel-ative to plant weight. It seems logical then to assume that not only was root growth of white oak seedlings actually greatest in the Orange area and smallest in the Congaree area but that the weight of root relative to plant weight may also have been greatest in the former area and smallest in the latter. This relation apparently did not hold for 1-year-old and 2-year-old seedlings of red maple or downy viburnum. To what extent the relation may be applied to the other species studied was not determined as data for 1-year seed-lings alone are not sufficient to enable any such con-clusion to be drawn. However, it is certain that there are significant differences in the actual root weight of the various species that grew in the three habitats. At this point there is no way to prove that differ-ences in weight of root relative to plant weight were due to the environment in which they grew instead of having been a result of a more or less natural trend of root weight relative to plant weight corre-lated with amount of total plant growth.

Although total length of secondary roots of some species was not greatest in the Orange area, most of the species showed definitely that such was the case and that total length was least in the Congaree area. The fact that total length of secondary roots did not always vary in proportion to root weight in the pres-ent studies seems to indicate that caution should ac-company the use of either measurement alone as an absolute indication of root development in any given environment.

The relative depths of root penetration of seedlings are not easily defined as several factors apparently controlled penetration in the three areas. Those species whose roots were confined to the A horizons

(loblolly pine, red cedar, red gum, red maple, and downy viburnum) showed either little difference in maximum depth of root penetration or a direct cor-relation with total growth of roots. Those species whose roots penetrated as deeply as the B_1 horizon (white oak, post oak, black oak, blackjack oak, and northern red oak) varied greatly in maximum depth of penetration. Few statistically significant differ-ences between mean maximum depths were obtained in the latter instances because of the variation.

The characteristic root habit of each species was the same in the three soils. However, from the pre-ceding paragraphs, it is apparent that root develop-ment was different in the three habitats. The factors which apparently influenced depth of root penetration of the seedlings in the present study will be discussed first and then those factors relating to root develop-ment on other bases will be discussed.

If the soils had been of the same degree of com-pactness, total root growth and maximum depth of penetration could have been expected to be somewhat directly correlated. However, from the data obtained concerning nature of the soils, it is apparent that they varied in degree of compactness. The B_1 horizon of the Orange soil was especially compact as is borne out by observations and actual data. The values for porosity (Table 5) and air capacity (Table 2) were exceptionally low for the Orange soil at that depth. It should be recalled that percolation rates were low-est in the Orange soil. Overemphasis should not be placed on the Orange soil, for the Georgeville soil was shown to have been the heaviest in clay (Table 1), especially in the B horizons, and to have had the greatest degree of aggregation of the three soils under consideration.

With these facts in mind the interpretation of max-imum depth of root penetration of seedlings is more easily understood. The impervious claypan in the Orange soil at a depth of 8 inches quite often marked the approximate limit to downward penetration of roots. Some were able to penetrate the horizon, usually by following a channel or cleavage furrow, and reach a depth even greater than in the other two soils where the claypan was lacking. The lack of penetration into the claypan is in accord with results found by Weaver and Crist (1922) in studies con-cerning the relation of root growth to a hardpan layer in the soil of the Great Plains region. Büsgen and Münch (1926) point out that roots cannot pen-etrate into subsoils which are compact. Markle (1917) and Taubenhaus (1931) found that penetrability of the soil was important in root development.

As has been pointed out, the lack of a claypan in the Georgeville soil does not mean that the soil was not compact as compared with the Congaree. In fact, measurements and observations indicate that root penetration was retarded by the B horizon of the Georgeville soil. Unless the roots followed some sort of break in the soil mass, they seemed to be able to penetrate less deeply into the substratum than in the Congaree soil that was less compact. Therefore it is not surprising that even with a greater growth of

roots (on a dry-weight basis) in the Georgeville than in the Congaree soil, average measurements indicate that penetration was greater in the Congaree than in the Georgeville soil. This is true of all average measurements made of species that penetrated as deeply as the B_1 horizon.

Variations in root development may be due to various environmental factors. Since certain factors vary in the three areas under study, their relation to root development on bases other than depth of penetration will be discussed. Finally, those factors that may account for the differences in root development will be evaluated.

Soils in which roots of the seedlings developed were different in texture, particularly in the A horizons. Mechanical analyses showed that the Georgeville soil was the most finely textured soil of the three in the present study. The work of Hassis (1921) and Pearson (1931) would lead us to expect root development to have been greatest in the Georgeville soil, while that of Savits (1882), Büsgen and Münch (1926), Anderson and Cheyney (1934), and McQuilkin (1935) would indicate that development would have been least. If texture had an effect one way or the other, such effect in this study was much overshadowed by some other factor; because although the Georgeville soil was finer textured than both of the other two soils, the seedlings had a greater root development than in the Congaree and a smaller development than in the Orange soil. Stevens (1931), Farris (1934), and Yeager (1935) have reported no correlation of root development with soil texture.

Aeration at various times was somewhat different in the three soils and had a definite effect on roots of the species of this study as has previously been indicated in a few instances, especially in regard to seedling establishment and survival and to seedling injury. The studies of actual air space in the soil, soil porosity, composition of soil air, and field percolation rates lead to the establishment of certain pertinent facts in regard to relative aeration in the three soils. These facts will be reviewed briefly to bring out more clearly their relation to root developments.

It was found that porosity of the Orange soil was the least of the three soils, particularly in the B_1 horizon. The Congaree soil, which because of its less compact nature might have been expected to have been most porous, was even less porous in horizon 3 than the Georgeville soil at the same depth. Porosity, of course, limits the ultimate amount of aeration possible.

The actual air space, which largely controls aeration, changed with amount of water in soil. This is confirmed by determinations of air space and water content of soil. Measurements of air space in the three soils at certain periods show that the Orange soil contained less air space than the Congaree which in turn contained less than the Georgeville. Field percolation rates, which indicate the relative number of waterways in the soils and accordingly probable air passageways, also suggest that air exchange was greatest in the Georgeville and least in the Orange

soil. Since carbon dioxide content of soil air has been shown to be inversely related to air space in soils, carbon dioxide content of the soils should, excluding other factors, have been greatest in the Orange and least in the Georgeville soils. This was true.

Concentrations of carbon dioxide were not found to be sufficiently high to have had much effect on root growth, unless the gas accumulated in pockets. The highest concentration found in the upper three horizons was 1.50 percent. As no determinations of gas concentrations could be made under extremely wet soil conditions, no data were obtained as to the concentrations of gases in the soil at those times. However, in view of the fact that carbon dioxide content of the soil air increased with total moisture content, it is believed that when the soils were very wet the carbon dioxide content was much higher than 1.50 percent.

During periods of heavy rain the upper horizons of the Orange and Congaree soils often become saturated with water, or nearly so. At these times it is believed that the carbon dioxide content probably was sufficiently high significantly to influence root growth.

Practically all of the deaths and injuries of roots in the Georgeville area could be attributed to certain specific causes other than aeration conditions, and therefore aeration was probably not an important factor in the death and injury of seedlings in the Georgeville soil. Although fungous infection was severe in the Orange soil and active in the Congaree soil, death and injury to seedlings was in all probability due, at least in part, to high carbon dioxide or low oxygen content resulting from poor aeration during periods of high soil moisture content. Death of plants caused by poor aeration has been shown by Graves (1915), Bergman (1920), and Turner (1922). High carbon dioxide content, as pointed out by Cannon and Free (1925), Cannon (1920), Hole (1918), and others, may cause death of or injury to the roots of plants. It has also been shown that low oxygen content may have the same effect (Turner, 1922; Cannon, 1920; Cannon and Free, 1925).

The amount of root development was shown by Biswell (1935), Cannon (1923), Cannon (1924), Cannon and Free (1925), Loehwing (1931 a, b), and Gail and Long (1935) to be influenced by aeration and air content; poor aeration, which tends toward low oxygen and high carbon dioxide content, resulted in smaller amounts of growth than under well-aerated conditions. The different aeration conditions of the three soils of this study probably did not cause the differences in the root development of uninjured seedlings growing in the three soils, because root development was greatest in Orange soil where aeration, as indicated by air space, has been shown to be least favorable and therefore should have restricted root development.

It cannot be said that the greater root development of the uninjured seedlings that grew in the Georgeville soil as compared with root development of those that grew in Congaree soil was not due, at least in part, to better aeration of the former soil. However,

in view of the fact that no such relation exists be-
tween seedlings from the Orange and Congaree soils,
it is very likely that differences in root development
of uninjured seedlings in the three soils were a result
of conditions other than those of aeration.

The number of roots in the top 18 inches of the
soils was shown by soil transects to have been differ-
ent in each soil (Table 8). The number of roots indi-
cates that there were probably differences in the
amount of root competition in the three areas. Root
competition has been shown to affect root develop-
ment. Adams (1928) found that crowding of jack
pine (*Pinus banksiana* Lamb.) seedlings increased
the penetration of roots but found no correlation with
relative amount of roots and tops that are developed.
Show (1930), however, shows that forest-tree seed-
lings in seed beds had a decreased amount of roots
in proportion to crowding.

On the basis of number of roots in the soils studied,
root competition apparently did not cause the differ-
ences in root development of seedlings. If it is as-
sumed that root competition did cause the differences,
then it would be necessary to explain the fact that
in the Georgeville soil, which had the least amount
of root competition of the three soils, seedlings had
greater root development than seedlings from the Con-
garee soil; and on the other hand, also had a smaller
root development than those from the Orange soil.

In view of the extremely large number of roots in
the upper 3 inches of the Orange soil, root competition
probably was the cause of the few instances in which
total length of secondary roots of seedlings from the
Orange soil was less than that of those from the
Georgeville soil. For example, in post oak and black
oak, even though the weight of root was greater in
the Orange area, the total length of secondary roots
was smaller. This seems to have been due to a lack,
in the upper few inches of soil, of roots on seedlings,
as appears on the post oak seedlings in Figure 3A.
Extremely low available moisture content in the upper
two inches of the Orange soil during periods of rel-
ative dryness (Figure 1) was probably due in part
to root competition, in part to a greater loss of water
either directly or indirectly through transpiration as
a result of greater evaporation, and in part to a lower
initial water content caused by a low water-holding
capacity. When available moisture is sufficiently low
it might cause the death of roots on seedlings and
even death of seedlings.

Evaporation from standard Livingston atmometers
at the three experimental areas was measured from
June to October, 1936 in studies made by members
of the Duke Forest Staff. The results show that
evaporation was greatest in the Orange area and
smallest in the Congaree. To what extent the relative
conditions of evaporation affected root growth of seed-
lings in the sites is not known. However, develop-
ment was smallest in the area in which evaporation
from Livingston atmometers was smallest and was
greatest in the area in which evaporation was greatest.

Studies of the chemical characteristics of the soils
in the three present (and other) areas were made by

Korstian and Coile (1938). The results indicate that
the three areas of the present study differed insofar
as their relative fertility levels are concerned; the
fertility as indicated by nitrates and carbon-nitrogen
ratios being best in the Congaree area and least in
the Orange area. Greater fertility apparently was
not directly correlated with root development in the
present study as an inverse relation existed between
root development and soil fertility.

The acid-base reactions of soils (Bates, 1934;
Watenpaugh, 1936) have been found to affect root
development under certain conditions. However, Coile
(1933) found that the acid-base reactions of the three
soils in this study did not differ greatly enough to
be a limiting factor in the distribution of forest types
on the soils. The pH varied mostly between 5.5 and
7.0. With such small variation it is thought that root
development of seedlings was probably not greatly
influenced by differences in the acidities of the soils
under consideration.

The relative amount of shading in the three areas
should be recognized as a possible factor in influencing
root growth of seedlings in the experimental areas of
this study. Cannon (1925), Wiedemann (1926),
Show (1930), and Biswell (1935) have shown that
root growth increased with increasing light intensity.
Korstian and Coile (1938) point out that light inten-
sities varied significantly within and between different
stands of their study; three of the stands being the
same as those of the present study. The Orange area
was more open than the other two areas and the Con-
garee the least open. This relationship is evident in
the stem and crown-projection maps presented by
Korstian and Coile (1938). The resulting lower light
intensities might possibly have brought about a de-
creased root growth of seedlings. At least, root de-
velopment was greatest in the area in which the
apparent light intensity was greatest and was smallest
in the area in which the apparent light intensity was
least.

It has been pointed out in the analysis of seedling
establishment and survival, that death of seedlings
may have been caused by death of their roots due to
total soil moisture acting indirectly through aeration.
Relative amount of injury to roots, because of poor
aeration, was indicated in the analysis of injury to
live specimens of each species. Also total soil mois-
ture acting indirectly through changes in aeration
has been pointed out as probably not having affected
root development of uninjured seedlings. Soil mois-
ture in its relative availability to seedlings, however,
may possibly have affected the amount of root devel-
opment of the seedlings growing in any one of the
three soils (Schwarz, 1892; Büsgen, 1901; Markle,
1917; Weaver, 1919; Weaver, 1925; Laitakari, 1929;
Holch, 1931; Sperry, 1935; and Reed, 1939).

The data obtained in this study show that as the
soils became dry the Congaree soil, at depths at
which roots of seedlings grew, usually contained the
greatest amount of available moisture and the Orange
soil the least (Figure 1). Since root development was
greatest in the Orange area and least in the Congaree,

there was apparently an inverse relation between available soil moisture and root growth.

EVALUATION OF IMPORTANT FACTORS IN RELATION TO ROOT DEVELOPMENT

Among the important factors influencing root development were the compact soils in certain horizons of the Orange and Georgeville areas. These soils apparently retarded root penetration. Root development was also affected by injury to seedlings as a result of the action of two other factors. First, in the shallow rooted species injury from heaving by frosts was undoubtedly important because of its influence on the roots. Secondly, injury by poor aeration and fungous attacks to roots of all species was evident, especially in the Congaree and Orange areas, and should not be underestimated in regard to root development.

Studies by Korstian and Coile (1938) indicate that during the growing season soil moisture was generally not above optimum in the three areas in the present study; trenched plots with a resultant increase in moisture content of soil supported a greater growth of vegetation than untrenched plots. Thus, the lower amount of available soil moisture in the Orange area may have reduced plant growth more than in the Congaree and Georgeville areas where there was generally more available soil moisture. However, since the development of both entire plants and tops was greatest in the Orange area, lower available soil moisture did not reduce plant and top development in the Orange area as much as other conditions checked growth in the Congaree and Georgeville areas.

It has been pointed out that texture, aeration, soil fertility, and acid-base reaction of the soils did not account for differences in total root development of uninjured seedlings. However, it seems logical to assume that the light available to seedlings may have been less in the Congaree and Georgeville areas and thus have reduced photosynthesis and consequently decreased amount of plant, top, and root development. Holch (1931) found a similar situation in the case of five species of forest-tree seedlings growing in three Nebraska habitats. Also the advantageous and disadvantageous reactions among the species growing in the three areas were perhaps not the same in each area and may thus have affected plant, top, and root development.

More intense light received by seedlings in the Orange area would tend to have produced a greater weight of root relative to plant weight than occurred here as compared with the other areas and might even have increased total root development. Greater light intensity has been shown to increase weight of root relative to plant weight (Shirley, 1929; Show, 1930). Also, greater transpiration (Cannon, 1925), as suggested by evaporation from Livingston atmometers, and less available soil moisture (Weaver, 1919) may have tended to increase the weight of root relative to plant weight.

The data in the present study do not indicate whether root growth was changed only relative to plant weight or whether weight of roots and weight relative to plant weight were changed by transpiration and soil moisture conditions. Considering this question from one aspect; greater root development at the expense of tops may have resulted from greater transpiration or lower available soil moisture and thus have increased total root development and weight of root relative to plant weight. Considering the question from another aspect; these factors may have decreased growth, particularly of the top, and thus have increased root development relative to plant weight, whereas the weight of root was either the same or less.

Thus, lower available soil moisture may have increased root development relative to plant development in the present study but may or may not have increased total root development. Most of the difference in total root development was a result of reduction in plant development in the Georgeville and Congaree areas. Differences in total root development might also, to a certain extent, have resulted from the effect of conditions other than edaphic, such as transpiration and light.

SUMMARY

1. A study was made of root development of seedlings of certain important woody species in three different soil types. The specific edaphic conditions causing variations in root development were determined as far as possible. The study was made in the Duke Forest in Durham and Orange Counties, North Carolina. The three soil types chosen for study are Congaree clay loam, Georgeville clay, and Orange loam. Experimental areas were established for each soil type.

2. To determine similarities and differences in the edaphic conditions on the three sites, certain measurements were made. Determinations of physical properties of the soils included water-holding capacity, air capacity, volume-weight, wilting percentage, field percolation rate, mechanical analysis, soil aggregation, soil air space, soil porosity, and soil atmosphere. The relative soil moisture conditions of the three areas were determined from measurements of total soil moisture obtained during the spring and summer of 1936, from May 5 to August 6. Average available soil moisture throughout this period was determined for the three soils and is presented in tabular and graphic form.

3. Soil analyses show that the Congaree soil was characterized by relatively large percentages of sand throughout the profile. The Georgeville was clayey throughout, particularly in the B horizons. The A horizons of the Orange soil were loamy and the B horizons were a very tightly packed, impervious clay. Aggregation of soil particles was pronounced in the Georgeville soil. The Orange soil showed less aggregation and the Congaree soil very little aggregation.

4. The mean water-holding capacities at 0 to 2 inches and 2 to 4 inches were greatest in the Congaree soil, least in the Orange, and intermediate in the Georgeville soil. At the lower depths at which deter-

minations were made the mean water-holding capacities were greater in the Georgeville soil than in the other two soils.

5. Determinations of wilting percentages were made on undisturbed soil from four depths in the three soils and the results presented in tabular form. The permanent wilting of oats was used to indicate the lower limit of available soil moisture.

6. The Congaree soil usually contained more available moisture than the Georgeville soil. When the soil moisture content was near the lower limit of availability the Orange soil usually had the least available soil moisture and the Congaree soil the most.

7. Determinations of mean air capacities at various depths in the three soils show that the B_1 horizon of the Orange soil was extremely low in air capacity as compared with all other determinations in the three soils. In addition, mean volume-weight of the B_1 horizon of the Orange soil was highest and porosity lowest.

8. Mean percentages of carbon dioxide and oxygen in soil air and of soil air space by volume, and moisture content of soil on a dry-weight basis were determined for four depths in the three soils, in April and October, 1935. Carbon dioxide content of soil air increased and oxygen content decreased with increased soil depth and with decreased air space. Carbon dioxide content was usually greatest in the Orange soil and least in the Georgeville. This was probably due to differences in air space; air space was least in the Orange and greatest in the Georgeville soil.

9. Relative field percolation rates indicate that the waterways and therefore probably air passageways were greatest in the Georgeville soil and least in the Orange soil. On this basis, aeration was best in the former and poorest in the latter. During periods of heavy rainfall, the Congaree and Orange soils were much more waterlogged than the Georgeville soil, and aeration was thereby reduced much more in the Congaree and Orange soils than in the Georgeville soil.

10. On the basis of number of roots of all sizes in the top 18 inches of the three soils root competition was least in the Georgeville soil and most in the Congaree soil.

11. Seeds of white oak, post oak, blackjack oak, black oak, scarlet oak, northern red oak, loblolly pine, red cedar, yellow poplar, dogwood, red gum, and sourwood were planted in seed beds in the three experimental areas in October and November, 1934. The seed beds were protected by one-fourth-inch mesh wire screen.

12. The number of seedlings of each species established in each seed bed was recorded on June 1, 1935. The total number established in the seed plots in the three soils was lower in the Orange soil than in the other two soils. The number of surviving seedlings was recorded on October 1, 1935 and May 20, 1936. Survival of most species was best in the Orange area and poorest in the Congaree area. Death and injury to the seedlings were due, in part, to infection by *Rhizoctonia* spp.; in part, to heaving during the winter of 1935-36 (species with deepest root penetration

being least affected); and probably, in part, to high carbon dioxide and low oxygen content of soil air during periods in which soils were at or near water-logged condition.

13. Excavations of seedlings were made in March and April, 1936. Drawings and careful observations of each seedling were made at time of excavation. Excavations of naturally seeded specimens were made in the late autumn of 1936 and in May, 1937 in order to augment these data. Excavation in the late autumn of 1936 were of seedlings that had completed their first summer's growth. Those in May, 1937 were of 1- and 2-year-old red maple and downy viburnum seedlings and of 2-year-old white oak. A total of 372 seedlings were dug to obtain the data in this study.

14. A study of the development of sourwood, yellow poplar, dogwood, and scarlet oak seedlings was omitted because available material was inadequate. Data were obtained for the ten remaining species, and except for blackjack oak, northern red oak, and red cedar were treated statistically. The data include measurements of total weight of plant, top weight, maximum depth of root penetration, total length of all secondary roots, and root weight. The weight of roots relative to total plant weight was also determined. Most of the differences between means of measurements from seedlings in the different areas were found to be statistically significant and are therefore probably a result of the environments in which the plants grew.

15. The data in most cases show that seedling development was greatest in the Orange area and smallest in the Congaree area. Root development on a dry-weight basis was also greatest in the former and smallest in the latter area. Differences in root weight were perhaps not always in proportion to the differences in plant weight. This is brought out by the data from 1- and 2-year-old white oak seedlings. Total length of secondary roots was usually greatest in the Orange area and smallest in the Congaree.

16. Those species whose roots were confined to the A horizon showed either little difference in maximum depth of root penetration or a direct correlation with total growth of roots in the three soils. Those species whose roots penetrated as deeply as into the B_1 horizon showed a varied response. The B_1 horizon of the Orange and Georgeville soils seemed to retard root penetration as compared to soil at the same depth in the Congaree area. Breaks in the soil mass of the compact B horizon were often occupied by roots enabling them to penetrate much more deeply than otherwise. The characteristic root habit of each species was the same in the three soils.

17. In this study, if the texture of the A horizon affected root development (on bases other than depth of penetration), it was much overshadowed by some other factor, because the amount of root development was not correlated with texture.

18. Different aeration conditions of the three soils in this study probably did not cause the differences in root development because root development was great-

est in the Orange soil where aeration was least favorable and would tend to have restricted root development more than in the other two areas.

19. On the basis of the number of roots in the three soils, root competition in this study apparently did not cause the differences in root development of seedlings.

20. Amount of evaporation from standard Livingston atmometers was greatest in the area in which root development of the seedlings was greatest and was smallest in the area in which root development was smallest.

21. Soil fertility as indicated by nitrates and carbon-nitrogen ratios apparently was not responsible for the differences in root development as an inverse relation existed between root development and soil fertility.

22. Acid-base reactions did not vary sufficiently between the three soils to have caused any appreciable variation in root development.

23. Relative amounts of shading in the three areas should be recognized as a factor which may have influenced root growth.

24. There appears to be an inverse relation between available soil moisture and root growth. The data in the present study indicate that lower available soil moisture may increase root development relative to plant development but do not indicate whether total root development is affected thereby. However, most of the difference in root development was a result of decreased growth of seedlings in the Georgeville and Congaree areas. Differences in total root development might also, to a certain extent, have resulted from the effect of conditions other than edaphic, such as transpiration and light.

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AN EXPERIMENTAL STUDY OF RHIZOMES OF CERTAIN PRAIRIE PLANTS*

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AN EXPERIMENTAL STUDY OF RHIZOMES OF
CERTAIN PRAIRIE PLANTS

INTRODUCTION

Since the coming of the prolonged drought with the attendant shift in plant populations, students of grassland ecology have become increasingly aware of the need of detailed information concerning vegetative propagation of prairie plants. Literature on the subject is limited both in quantity and in scope. General descriptions and a classification of the subterranean organs of several species of plants from the vicinity of Manhattan, Kansas, were published by Hitchcock (1899, 1900). Hayden (1919) included studies of rhizomes in her investigation of the ecologic anatomy of some plants in central Iowa. Weaver (1919, 1920) and Weaver and Fitzpatrick (1934) have included observations and descriptions of rhizomes in their extensive studies on grasslands. Among the few sources of information on rate of spread are the studies of *Helianthus scaberrimus* (Cooper and Stoesz, 1931), *Agropyron repens* (Kephart, 1931), *Buchloe dactyloides* (Savage, 1934), and *Convolvulus soldanella* (Purer, 1936). Similar information for woody plants has been published by Duncan (1935). Kerner (1898) and Warming (1918) have furnished this type of data for several European species. Emerson (1921) studied form, physiological relationships, and factors involved in horizontal placing of roots and rhizomes of bog plants. Dexter (1936, 1937) investigated responses of rhizomes of *Agropyron repens* to various injurious factors. Salisbury (1929) reviewed the factors influencing rate of growth and robustness of rhizomes.

Very early studies of rhizomes were morphological and anatomical. The first physiological studies appeared from 1870 to 1880 when Schwendener, Haberlandt, and Falkenberg correlated structure with the laws of physiology, Duval-Jouve traced the history of rhizome reserves in *Panicum vaginatum,* and Royer stated the law of level. Later studies concerning the morphology and physiology of rhizomes include those of Costantin (1883) on dicotyledons, Rimbach (1902) on California Liliaceae, Dauphine (1903) on law of level, François (1908) on aquatic plants, and Chaillot (1914) on mints.

The present investigation of rhizomes of certain prairie plants had several objectives. The development of the rhizome was to be traced from the seedling to the adult stage of the plant and, in the adult, through a complete annual cycle. Rates of vegetative spread were to be determined for plants growing in two types of soil. Responses of rhizomes to such adverse environmental conditions as exposure to dry air or burial beneath soil deposits were to be ascertained for certain species. Additional details were to be secured to supplement known general descriptions.

Writers are not in agreement concerning the concept of a rhizome. Most often the term is applied only to horizontal subterranean stems. A broader interpretation was recognized by Brenchley (1920) and adopted by Hayden (1934). In this latter sense a rhizome is any somewhat uniformly thickened underground stem. Its direction of growth may vary from horizontal to vertically ascending or descending, and its source of origin may be from either the epicotyl or the hypocotyl of the seedling, or from the root. The broader concept is the one adopted for this study. The term stolon refers to any horizontal stem at or immediately above the ground level. The property of a plant, equipped with tubers, bulbs, or rhizomes, to accumulate its underground reserves at the same depth under the same given conditions is known as the law of level.

The writer wishes to express appreciation for the valuable guidance of Dr. J. E. Weaver who suggested and directed the problem.

GEOLOGY AND SOILS

Field investigations, involved in this research, were confined to Merrick County, Nebraska, which is in the east-central section of the state and about 90 miles northwest of Lincoln. The Platte River forms the southeastern boundary of the rough triangle to which the county may be likened. Most of its area is comprised of the flood plains and terraces of the Platte and Loup Rivers, separated by sand hills.

Many geologists have considered the Platte River an aggrading stream and its valley an alluvial plain. Lugn (1935), in his study of the Pleistocene Geology of Nebraska, has shown that the Platte has been an eroding stream and that the "Platte River" sand and gravel is an exposure of a great fluvio-glacial deposit which is continuous over 15,000 or more square miles in south-central Nebraska.

The oldest formation of the Pleistocene period underlying Merrick County is known as the Holdrege formation. It is not exposed anywhere in the county. It consists of sand and gravel which are believed to have been transported by rivers from the west and northwest. In addition, it contains outwash material from the Nebraskan Glacier. Overlying this is the Fullerton formation. This is a layer of calcareous silt and clay probably deposited during the Aftonian interglacial age. This has been found to be as much as 58 feet thick in the western part of the county. Peat deposits and forest growth have been found on the upper surfaces of the Fullerton clay in deep gravel pits in the vicinity of Central City. A second sheet of sand and gravel covers the Fullerton formation. It is known as the Grand Island formation and is the Kansan counterpart of the Holdrege sand and gravel. The upper 30 to 50 feet of this sheet is fine

sand and the lower part contains much coarse sand
and gravel. The sand hills between the Platte and
the Loup valleys have been formed by Recent wind
action on the sand from the upper part of the Grand
Island formation. The Platte River has entrenched
itself in the coarser material of the Grand Island
formation and has not been able to erode farther.
Its competency was decreased because of greater
losses of water brought about by increased percola-
tion and seepage. The Grand Island sheet was cov-
ered by the Upland which is similar in origin to the
Fullerton and this in turn by the Loveland and
Peorian Loess formations. The erosion of the lower
Platte River Valley is post-Loveland and pre-Peorian
in age. The Loveland loess is found on the bluffs
lying on the Upland formation but never mantles the
eroded side-slopes or occurs on terraces or the river
flood plain as does the Peorian. Remnants of Peorian
loess are found in the northwestern part of the county,
lying in contact with the Grand Island sand. Other
remnants in the same vicinity are covered with Recent
dune sand. The loess deposit has been eroded from
the greater part of the county.

As the preceding geologic story would indicate,
most of the soils in Merrick County contain consider-
able sand. These soils have developed in a grassland
climate with an average annual precipitation of about
25 inches. The calcium carbonate horizon which
characterizes soils of the drier regions is evident only
in the western part of the county. Descriptions of
the soils at each of the five stations, where under-
ground parts of plants were studied, are based on
the Soil Survey of Merrick County, Nebraska (Hayes
et al., 1926). They are given in connection with the
location and description of stations.

CLIMATIC CONDITIONS

In general, climatic conditions are such as to place
Merrick County in the transition between True Prairie
and Mixed Prairie. The mean annual precipitation
is about 25 inches with the heaviest rainfall normally
occurring in spring and early summer. Periods of
drought are common in August and September.
Humidity is relatively low, frequently falling to 25
or even 15 per cent on afternoons of hot summer days.
Evaporation is high, and the proportion of days of
sunshine is great. The average length of the frost-
free season is 158 days. There is considerable range
in both seasonal and daily temperatures. Those on
summer days are regularly 80 to 100° F. and they
have risen as high as 114° F. Extreme winter tem-
peratures of —26° F. and daily variations of 46° F.
have been recorded at the Weather Bureau station at
Central City.

There was nearly a 6-inch deficiency in precipita-
tion in 1937. The soil was so dry by late summer
that it was necessary to water the plants when they
were transplanted into experimental gardens. Good
rains in September somewhat ameliorated the drought.
On the whole, moisture conditions were favorable in
1938. Total precipitation was 23.5 inches and only

1.5 inches below normal, and there was but one week
without rainfall from the first of May until the first
of October. The winter and spring of 1938-1939
were very dry, but beginning about May 20 and con-
tinuing through the first week of July, rainfall was
normal and favorably distributed. The second week
in July marked the beginning of drought which, ex-
cept for a few showers, continued until October when
the experiment was completed (Fig. 1).
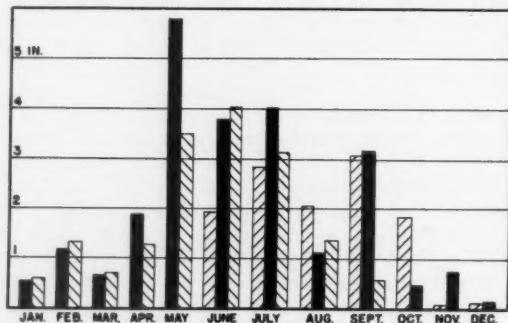
FIG. 1. Precipitation in inches during June to Decem-
ber 1937 (left hatch), 1938 (solid black), and January
to October 1939 (right hatch) at Central City, Nebraska.

The growing seasons both in 1938 and 1939 were
longer than average. In 1938 there were 168 con-
secutive days free from frost. For hardy perennials,
such as prairie grasses and forbs, the actual growing
season usually begins far in advance of the last spring
frost. In 1939, there were no killing frosts after
April 21 nor before September 30. Photosynthetic
activity, no doubt, was inhibited by periods of mois-
ture deficiency and high temperature in midsummer.
Temperatures were higher in 1939, but the period
with mean maximum temperatures above 90° F. was
shorter than in 1938.

LOCATION AND DESCRIPTION
OF STATIONS

Studies of seedlings and certain experiments were
conducted in a greenhouse at Lincoln. Of the five
field stations maintained in Merrick County, one was
in a garden at Central City and a second was on waste
land near the Prairie Creek Church, 8 miles westward.
The soil at both stations is known as O'Neill sandy
loam. The grayish-brown surface layer is very po-
rous. At a depth of 10 to 15 inches, it passes abruptly
into a loose sand containing very little organic matter.
This becomes coarser with depth and below 30 inches
consists largely of coarse sand and gravel. Lime is
absent in both soil and subsoil. The Prairie Creek
Church station is a portion of a timber claim and was
once planted to cottonwood trees. Prolonged drought
had reduced the mature trees to a few whitened skel-
etons. Extensive communities of several species of
prairie forbs and grasses were found in pure stands.
Quadrats were established and vegetation covered
with soil deposits.

Similar quadrats were located in Dune sand on an unused roadway between two pastures in the southeastern corner of Loup Township. The roadway had never been graded and except for grazing or cutting at infrequent intervals the vegetation was undisturbed. The fine to medium sand of this locality extends, with little change, to a depth of 3 or more feet. There is a small quantity of organic matter near the surface. Depressions between dunes contain sufficient organic material to give the topsoil a dark color. Tall grasses, such as *Andropogon furcatus, Panicum virgatum,* and *Sorghastrum nutans,* grow luxuriantly in these depressions.

The two remaining stations, both experimental gardens, were established in fields that had been tilled, one for 45 and the other for 65 years. The first field was in the sand hills near the western border of Merrick County and the latter was located on the flood plain of North Prairie Creek about 3 miles to the southeast. Both fields had been sown to wheat the previous autumn. The sand-hill garden was at the top and on the southeast slope of a gentle elevation. A small grove of red cedars (*Juniperus virginiana* L.) grew about 200 feet northward. The trees had been transplanted 25 years previously to check wind erosion of the sand. The field was not plowed following harvest, but annual weeds were removed by hoeing before plants were transplanted. The soil, a Hall fine sandy loam, has been highly modified by sand blown from surrounding Valentine and Dune areas. The topsoil is light colored and very sandy. The subsoil contains considerable yellowish clay which hardens upon drying. Hall fine sandy loam is highly calcareous below 20 inches.

The field in the bottom lands was plowed late in July, and the area chosen was free from perennial weeds. Trees which bordered the nearby stream were not sufficiently close either to shade the plants or to deplete soil moisture. The soil, classified as Lamoure very fine sandy loam, developed under conditions of poor drainage. The black surface layer, containing an abundance of organic matter and much silt, is 8 to 12 inches deep. The subsoil is a grayish-brown, very fine sandy clay of compact structure underlain at about 18 inches by mottled gray and white material of similar texture and structure. This extends to a depth of more than 3 feet. The surface soil is slightly calcareous and the subsoil has a high lime content.

METHODS AND PROCEDURE

Seeds of 10 species of grasses were sown in the greenhouse. A bench with a depth of 18 inches was filled with silt-loam potting soil. Seeds were sown in small plots and covered lightly. The soil was covered with strips of wrapping paper to prevent rapid drying. These were removed when sprouts appeared. The soil was kept free from weeds and the grasses thinned to reduce competition. Other conditions for growth were maintained as near optimum as possible.

Plants of each species were examined for rhizomes and stolons when they were at the approximate ages of 20, 28, 62, and 103 days. To ascertain the rate of growth of stolons of buffalo grass (*Buchloe dactyloides*), two plants were selected and the length of each stolon recorded daily for a period of 10 days. Species studied were *Andropogon furcatus* Muhl., *Bouteloua curtipendula* (Michx.) Torr., *Bouteloua gracilis* (H.B.K.) Lag., *Buchloe dactyloides* (Nutt.)· Engelm., *Calamovilfa longifolia* (Hook.) Scribn., *Panicum virgatum* L., *Phalaris arundinacea* L., *Poa pratensis* L., *Sorghastrum nutans* (L.) Nash., and *Spartina pectinata* Link.

Twenty-three species of prairie grasses and forbs were selected for the gardens. Twenty-one were duplicated in the two gardens. *Steironema ciliatum* (L.) Raf. was planted only in loam and *Solidago rigida* L. only in sand. Other species used were *Agropyron smithii* Rydb., *Andropogon furcatus* Muhl., *Andropogon scoparius* Michx., *Bouteloua curtipendula* (Michx.) Torr., *Bouteloua gracilis* (H.B.K.) Lag., *Buchloe dactyloides* (Nutt.) Engelm., *Calamovilfa longifolia* (Hook.) Scribn., *Elymus canadensis* L., *Panicum virgatum* L., *Phalaris arundinacea* L., *Poa pratensis* L., *Sorghastrum nutans* (L.) Nash., *Spartina pectinata* Link., *Apocynum sibiricum* Jacq., *Artemisia gnaphalodes* Nutt., *Aster multiflorus* Ait., *Aster salicifolius* Lam., *Polygonum muhlenbergii* S. Wats., *Solidago altissima* L., *Solidago glaberrima* Martens., and *Urtica gracilis* Ait.

Thrifty clumps or sods of each species were selected. These were removed with considerable soil and protected from excessive water loss while in transit to the gardens. Grasses which formed dense sods were cut into small, uniform pieces with diameters of 2 or 3 inches. Culms were clipped and 9 pieces were transplanted into each garden. Holes were dug deep enough to adjust the level of the sod with that of the soil in the garden, thus placing underground parts at their original depths. Water was added and soil packed firmly about each sod. The transplants were arranged in square plots with clumps 3 feet apart (Fig. 2). Paths between plots were 6 feet wide. Grasses forming open sods, such as wheat grass (*Agropyron smithii*) or slough grass (*Spartina pectinata*), and all the forbs were separated into single plants with roots and 2 or 3 thrifty rhizomes. All transplanting was done during the first week in September, 1937.

Heavy winter losses of *Phalaris arundinacea, Artemisia gnaphalodes, Aster multiflorus, Solidago glaberrima,* and *Apocynum sibiricum* in loam and of all but the first plus *Calamovilfa longifolia* in sand necessitated replanting of these species. This was done during the first week in June, 1938. Both gardens were kept free from weeds. Percentage survival, basal diameters of clumps (or length and breadth of areas occupied), and the general condition of plants were recorded early in September, 1938.

Final records concerning plants in both gardens

Fig. 2. Two-year-old bunches of little bluestem *(Andropogon scoparius)* in the sand-hill garden, showing the arrangement of plants in the plot. The average basal diameter increased from 2 to 8 inches in two years.

were taken between August 11 and October 1, 1939. Condition of plants, height, diameter, and total number of stems, and area occupied by stems were recorded for each species. Stem counts of buffalo grass and bluegrass were not made. In species with clumps still clearly defined, soil was removed from the base of each clump to expose completely the radial advance of the rhizomes, precautions being taken to keep the rhizomes intact. The basal diameter with rhizomes exposed was determined and from this the area occupied by rhizomes was computed. The depth range and the average diameter of rhizomes were recorded for each species. One or two average clumps of each species were removed from the soil, care being taken not to lose any rhizomes. The number of new rhizomes (those formed during the current season) was ascertained and the total length of all rhizomes in the clump was determined. From the data obtained. the number of new rhizomes per aerial stem and the length of rhizomes in feet per square meter were computed.

Species with propagative methods efficient enough to occupy an area so thoroughly as to obliterate the position of the nine original clumps were treated somewhat differently. The advance of the rhizomes beyond the periphery of the area occupied by stems was determined, after which the rhizomes were removed from a measured area, usually about one-fourth of the whole. Otherwise data were secured and computed as before. Extensive data were not obtained for underground parts of buffalo grass since it propagates chiefly by stolons. The area occupied and the thickness of the mat of grass were determined. The grass was clipped close to the soil, air dried, and weighed. One square meter taken from the heaviest portion of the mat was dried and weighed separately, and the production of forage in tons per acre was computed (Fig. 3).

A form of denuded quadrat was used to determine

ability of several species to recover through soil deposits of varying depths. Quadrats of western wheat grass *(Agropyron smithii)*, blue grama *(Bouteloua gracilis)*, many-flowered aster *(Aster multiflorus)*, prairie sage *(Artemisia gnaphalodes)*, and smooth goldenrod *(Solidago glaberrima)* were located at the Prairie Creek Church station; one for slough grass *(Spartina pectinata)*, in North Prairie Creek bottoms; and those for sand reed-grass *(Calamovilfa longifolia)* and big bluestem *(Andropogon furcatus)* at the Loup Township station. Plots 6 meters long and 1 meter wide were used for western wheat grass and for slough grass. These were enclosed by board frames. Two partitions were inserted to divide each into three sections, 2 meters long and 1 meter wide. At one end the board frames were 3 inches high, in the center 6 inches, and at the opposite end 12 inches. For all other species, square meter frames of the desired height were used. These were constructed in advance and were more convenient.

All the grasses were clipped before the frames were filled with soil. Soil was packed carefully around the intact stems of the forbs so that the leafy tops could continue activity above the deposit throughout the remainder of the summer. Topsoil from the vicinity of the quadrat was used for cover. This soil was loose and at first penetration of air was rapid. After compaction by rains additional soil was deposited to bring the layer to its proper level. So far as possible, the quadrats were located in communities of pure stand. The experiment was begun the second week in June, 1938, and completed one year later. Deposits 3, 6, and 12 inches in depth were used for most of the grasses and 3 and 6 inches in depth for the forbs. The 3-inch depth was omitted for *Calamovilfa longifolia* and the 12-inch for *Bouteloua gracilis*. At the end of the year each quadrat was plotted and the stems counted. Stem counts were also made in control quadrats located nearby. For examination of underground parts, a trench slightly deeper than the maximum depth of the underground stems of the experimental species was dug along one side of each

Fig. 3. Mat of buffalo grass *(Buchloe dactyloides)*, 7 inches thick, formed after stolons could no longer gain contact with the soil.

quadrat, after which the board frame was taken away and the soil carefully removed from the rhizomes. Mode of recovery was determined, and recorded by drawings.

It was discovered that rhizomes of *Polygonum muhlenbergii* could be exposed to the desiccating action of air for a considerable period of time without appreciable loss in turgidity. This suggested an experiment to determine the time that these rhizomes could be dried and still retain sufficient vitality to grow when placed in moist soil. Rhizomes were excavated and tested at three different periods in the development of the plant. The first lot was dug early in spring before the shoots were above ground. These were cut into pieces 3 and 6 inches long, respectively, each with a node. Both length-groups were divided into 5 lots of 12 pieces each. Controls were planted immediately in ordinary potting soil in the greenhouse. Others were exposed to the air in the laboratory 18, 44, 68, and 115 hours, respectively, before planting. A second group was dug when tops were 6 inches tall. After cutting into 6-inch pieces, these were divided into four lots of 12 which were dried 0, 22, 46, and 52 hours, respectively. A fifth lot of 24 pieces was dried 70 hours. The last were taken up June 18 when tops were 2 feet tall. The method of treatment was as before except that plantings were in the garden at Central City. Periods of exposure were 0, 24, 46, and 74 hours. Similar tests were made with rhizomes of western wheat grass. These were excavated in August and in June and tested in the garden at Central City. The experimental period was about one month, after which the rhizomes were examined for sprouts. The soil was kept moist at all times.

Investigations were not confined to the experiments just described, but underground stems of a great many plants were examined as they grew under natural conditions. Equipment consisted of a spade and a trowel for removing soil, and an ice pick and a tire iron for loosening it. When rhizomes were deep, a trench was dug to facilitate removal of soil. The trowel was used to clear away surface soil from rhizomes of small plants. As soon as radial extension of rhizomes of these plants was revealed, the whole clump was lifted with the spade and allowed to fall a short distance to loosen the remaining soil. It was sometimes possible, where extensive mats were formed, to expose the periphery of the rhizomes with a trowel and then, holding the flat side of the spade parallel to the soil surface, cut the roots below the rhizomes. After shaking out the soil, the stems were rolled back and the process continued until the whole mat was loosened. Field notes of a descriptive nature were based on these investigations. Normal levels, yearly advance, attachment of roots, length of internodes, diameter, color and character of scales were all noted. Many drawings were made in the field. Frequently information as to position, depth, etc., was noted in the field and the specimen taken to the laboratory for drawing.

EXPERIMENTS AND RESULTS WITH GRASSES

AGROPYRON SMITHII

Western wheat grass *(Agropyron smithii)* was found only sparingly in the eastern prairies until after the advent of the drought period which began in 1934, although it has always been abundant on the hard soils westward. Since then it has made remarkable inroads into areas left bare by death of other species or those disturbed by drifting soil (Weaver and Albertson, 1936). Its habit of growth is well adjusted to the distribution of rainfall. Growth is renewed early in spring and maturity is normally attained by mid-July when rainfall becomes less favorable. If the soil becomes dry, wheat grass is semidormant until fall rains stimulate new growth. Otherwise, growth continues throughout the summer. Examination of underground parts at frequent intervals during a growing season revealed that the growth periods of rhizomes were correlated with those of tops. New rhizomes began to form as early as the shoots provided sufficient food. Some attained a length of a meter or more and branched to produce other culms by the time flower stalks reached maturity. But when severe drought occurred, the food reserve was concentrated just back of the terminal bud while the remainder of the rhizome appeared wilted. The rhizomes again became active with return of moisture. They showed considerable resistance to drying effects of air. Of those excavated in June, 20 percent of the lot exposed 46 hours produced sprouts. Those tested the preceding August, however, failed to survive after even short periods of exposure (Table 1). Higher temperature and lower humidity may account for this complete loss of viability.

TABLE 1. Response of rhizomes of western wheat grass to desiccation.

Period of exposure (hours)	Length of rhizomes (inches)	Number planted	Per cent which grew
Excavated August 15			
0	6	12	50
24	6	12	0
48	6	12	0
72	6	12	0
Excavated June 18			
0	10	31	48
3	10	32	75
6	10	31	61
24	10	30	30
46	10	30	20

The slender rhizomes, glistening white when young and straw colored when mature, were much branched and interwoven into a coarse mesh which occupied the soil from depths of 1.5 to 5 inches. The length of the internode varied from 1 to 3 inches. Scales,

which soon split along the veins into long threads, were about as long as the internodes. The roots grew out from the nodes very much as the spokes radiate from the hub of a wheel. They mostly were directed laterally or downward. The rhizomes, 1 to 2 mm. in diameter, were usually more slender near the point of origin than near the sharply tapered terminal bud.

Many plowed fields lost considerable soil by wind erosion after the dry summer of 1937. One drift of soil was found the following summer completely clothed with western wheat grass, much of which was producing flower stalks. Examination showed that recovery had been made from the sod beneath through a deposit 10.5 inches deep. The parent rhizomes were found at a depth of 3 inches below the former soil level. Many branches had not yet reached the surface of the drift. No seedlings were found. In quadrats covered with soil, wheat grass was able to grow through a deposit of 12 inches (Fig. 4). Many
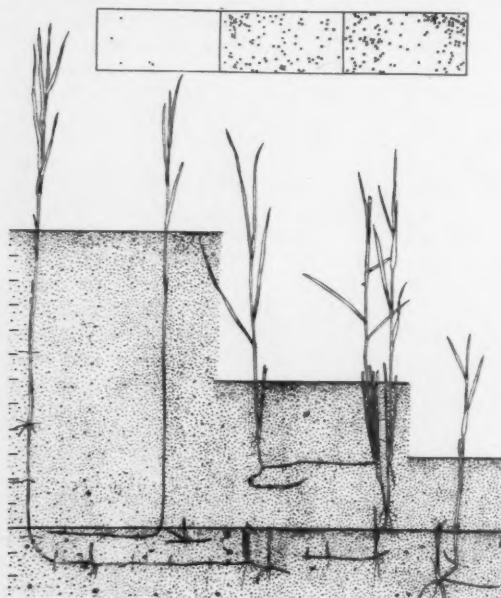
FIG. 4. Recovery of western wheat grass (*Agropyron smithii*) through soil deposits of 12, 6, and 3 inches depth. These plots each included an area of 2 square meters and yielded 5, 109, and 129 culms, respectively, as is shown in upper portion of the figure. Parent rhizomes are shown below the original soil surface.

of the old rhizomes in the soil beneath the new layer were still viable at the end of a year and were sending up feeble sprouts. Several culms in the quadrats with 3 and 6 inch deposits of soil were fruiting.

At North Prairie Creek, western wheat grass made a greater average gain in area, 53.8 sq. ft., than any other grass and was surpassed only by one forb, *Apocynum sibiricum*, which propagates by offshoots from horizontal roots. The response of this grass to conditions in sandy soil was quite different. While the total gain in area was about one-fourth as great,
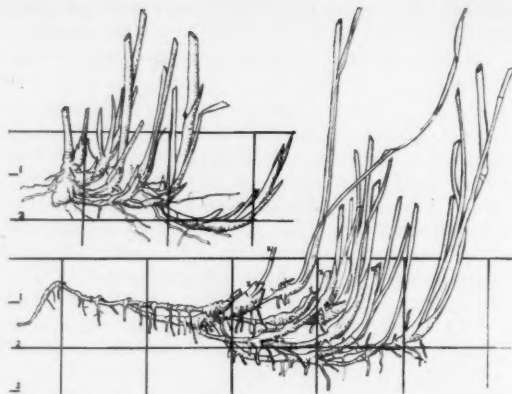
FIGS. 5 and 6. Fig. 5 (upper left). Rhizomes of Indian grass (*Sorghastrum nutans*) as they appeared late in summer. The terminal bud of the new rhizome lies close to the surface of the soil, but the horizontal portion is about 2 inches deep. Fig. 6 (lower). Habit sketch of the gnarled rhizomes of big bluestem (*Andropogon furcatus*), scale in inches at left. The annual radial advance, as indicated by the distance between old culms (X) and the new ones, is only 1 to 3 inches.

the stem production was only one-twenty second of that in loam. At North Prairie Creek, foliage was 25 inches and fruiting culms 37 inches tall. Growth was so rank that the plants lodged during a storm late in June. In the sandy plot, foliage was but 7 inches tall and no flower stalks were produced. Length of rhizomes included in a square meter was nearly 13 times greater (619 feet) at North Prairie Creek. This production was the greatest of any species. New rhizomes were often found advancing under neighboring plots of aster, bluegrass, and buffalo grass, where they attained a maximum length of 80 inches.

ANDROPOGON FURCATUS

A sod of big bluestem (*Andropogon furcatus*), clipped and washed free from soil, revealed a close network of gnarled rhizomes. Unlike most of the grasses included in this study, greatest radial advances were made early in spring. During the summer, food materials were concentrated in the rhizomes. Numerous buds near the bases of the culms became swollen and some attained a length of 5 to 6 mm. by the close of the growing season. These remained dormant until growth activity was renewed the following spring. Some developed immediately into shoots while others produced horizontal rhizomes, 1 to 3 inches long, before the terminal buds assumed a vertical position (Fig. 6). Under favorable conditions, new leafy shoots continued to appear throughout the summer. Small advances were made in this manner.

Rhizomes occupied the upper 2 inches of soil. Internodes were short, and the diameter was about 3 mm. The diameter of the roots, which are attached at the nodes, was nearly as great as that of the rhizomes. The dark scales, which became shredded

as the rhizome aged, were much longer than the internodes.

Seedlings developed rapidly. Those grown in the greenhouse began tillering in 3 weeks (Fig. 7). By

Fig. 7. Seedling of big bluestem (*Andropogon furcatus*) at the age of 28 days with seed and seminal root (S) still attached. Scale, 1 inch. Early and prolific production of tillers gives this species considerable competitive advantage. No advance was made by rhizomes before renewal of growth in spring.

the end of 9 weeks, stems were 3 feet tall and flowering. Of the 15 seedlings that were found in the vicinity of the plot at North Prairie Creek, 7 flowered and attained a height of 46 inches by September. One bunch included 20 flower stalks.

Andropogon furcatus showed a limited ability to grow through soil deposits. Three months after the quadrats had been covered, 7 stems had grown through 3 inches, 2 through 6 inches, but none through 12. The following spring, 570 stems appeared in the control quadrat, 89 stems pushed through 3 inches of soil, but there were none in either of the other quadrats. Removal of soil from the underground parts revealed that there had been no production of horizontal rhizomes at a normal level, although shoots had ascended from the level of the old rhizomes (Fig. 8).

Stems of plants grown at North Prairie Creek were from 12 to 20 inches taller than those grown in sand. Otherwise, there were no outstanding differences be-
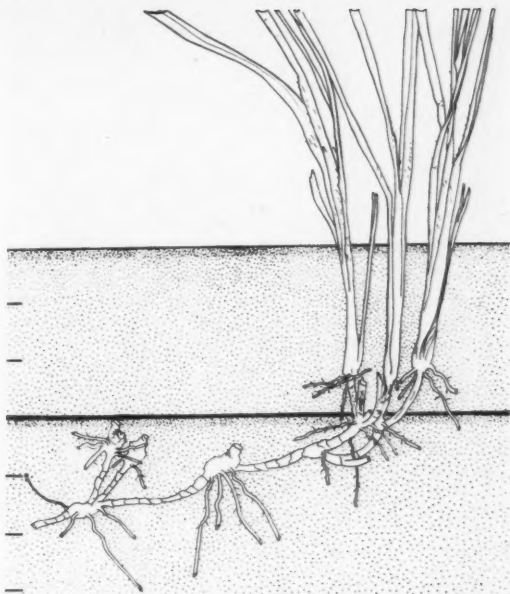
Fig. 8. Vertical ascent of rhizomes of big bluestem (*Andropogon furcatus*) through 3 inches of sand deposited the previous year. The annual cycle of rhizome development in this species indicates that a period including two vernal seasons would be required for development of horizontal rhizomes at a normal level.

tween the two plots. In loam, each clump gained 0.5 sq. ft. in 2 years, while those in sand each gained 0.4 sq. ft. Culm production was the same in both. The total length of rhizomes in a square meter of sod grown in loam was 319 ft. No determination was made from plants growing in sand.

Andropogon scoparius

The short, branched rhizomes of little bluestem (*Andropogon scoparius*) had internodes only 1 to 2 mm. long. Buds were usually inconspicuous but some became slightly swollen by late summer. These produced rhizomes and shoots the following spring (Fig. 9).

Each of the 6 clumps which survived in the garden at North Prairie Creek made an average gain of 0.6 sq. ft. in 2 years. This was slightly greater than the gain made by big bluestem. In 1939, each clump produced about 317 stems with a height of 41 inches. The rhizome production totaled 309 ft. per sq. m. The average gain of each of the 9 clumps in sand was 0.5 sq. ft., but average stem count mounted to 397 (Fig. 2). These plants were 32 inches tall. Eight seedlings, none of which flowered, were found in the plot of loam soil.

Bouteloua curtipendula

Seeds of side-oats grama (*Bouteloua curtipendula*), sown in the greenhouse, germinated quickly. Sprouts appeared above ground within 3 days. Tillering, which began in 3 weeks, continued at a rapid rate.

FIG. 9. A single branch from a clump of little blue-stem *(Andropogon scoparius)*, showing a well-developed rhizome at a depth of .5 inch. This grass is often cited as one lacking the rhizome habit.

FIG. 10. Portion of a seedling of side-oats grama *(Bouteloua curtipendula)*, showing a well-developed rhizome 64 days after germination (upper left). A typical branch taken from a mature plant (right). Development of new rhizomes, .5 to 2 inches deep, coincided with the season most favorable for growth of tops.

Plants, 9 weeks old, had produced from 20 to 40 stems and numerous rhizomes, many of which were nearly 2 inches long (Fig. 10).

Rhizomes of this species were fairly short and confined to the upper 2 inches of soil. None exceeding 3 inches were found, but Weaver, in grassland studies covering a broader area, has recorded lengths of 5 inches (Fig. 11). The diameter was slightly greater just back of the terminal bud than elsewhere; the average was about 2.5 mm. Scales were much longer than the internodes, consequently, the stem was not exposed until scales had been lost. They fitted closely at the margins but bulged elsewhere. This condition, combined with alternate attachment, gave the rhizome a zigzag outline. New rhizomes began development early in summer, the roots growing only at the nodes.

Seven of the original plants survived in each gar-den, those in the sandy plot being more robust. Some flowering stalks were 40 inches tall. Total increase in area per plant was 0.4 sq. ft. in both sand and loam. Stems were more closely aggregated in the sand, the 7 plants producing a total of 1,940 stems as contrasted with 837 in loam. The ratio of stems to rhizomes was 10 to 7 and the production of rhizomes

FIG. 11. Side-oats grama *(Bouteloua curtipendula)* grown in thin soil overlying limestone with rhizomes 2 to 5 inches long. Photo by Weaver.

was 331 ft. per sq. m. at North Prairie Creek. Total length of those in sand was not measured, but from the closer aggregation of stems it was estimated that production was nearly twice that in loam. Several seedlings were found at North Prairie Creek. Some were more than 30 feet from the parent plot.

BOUTELOUA GRACILIS

Seedlings of blue grama *(Bouteloua gracilis)*, like those of side-oats grama, developed very rapidly. They tillered within 21 days and produced flowers when only 2 months old. One plant, 60 days old and with a basal diameter of 1.5 inches, produced 32 stems. When the clump was broken, short rhizomes, about 0.5 inch long and giving rise to several upright stems, were revealed (Fig. 12). Examination of

FIG. 12. Blue grama *(Bouteloua gracilis)* 27 days old (left) with seed and seminal root (S). Well-developed rhizome from plant 63 days old (right). Length of scale, 1 inch.

FIG. 13. Habit sketch of blue grama *(Bouteloua gracilis)*. The well-branched rhizome, which advanced from .5 to .75 inch per year, is about .5 inch deep.

plants taken from native grassland showed that the yearly radial advance underground was from 0.5 to 0.75 inch (Fig. 13). The radial increase per year of clumps grown in the experimental gardens, however, was nearly 2 inches (Fig. 14). Many buds were developed at the base of each culm which produced a much-branched rhizome covered by shredding scales. Nodes were only about 2 mm. apart and the average diameter including scales was about 3 mm. A 44 percent loss of plants in sandy soil was due to exposure of roots by erosion. The average diameter of the remaining clumps was 1.6 inches greater than the diameter of those grown in loam.

Great areas of short-grass vegetation in midwestern ranges were smothered when soil deposits were formed

FIG. 14. Clump of blue grama *(Bouteloua gracilis)* with basal diameter of 9 inches after two years in the North Prairie Creek garden. Original diameter was 1.5 inches.

by the dust storms of recent years. Weaver and Albertson (1940) found that even an inch of dust caused the death of much of the short grass and that a covering of 2 inches or more was nearly always fatal. One instance of recovery of blue grama through a soil deposit of 2 inches is recorded from a prairie near Clay Center, Nebraska (Robertson, 1939). It was growing on low ground and had been favored by some run-in water. Eight bunches of this grass in a square meter quadrat grew through a 3-inch layer of soil. Recovery was made immediately and the new bunches fruited the same year. Rhizomes ascended almost vertically from the periphery of the parent crowns (Fig. 15). Usually each plant produced a ring of several small bunches. These results must be considered in the light of the following facts: the grass was covered at a time of great growth activity, when a food reserve was present, and before maturity had been attained; it had not been weakened by grazing prior to the experiment; soil moisture was plentiful during the first weeks of the experiment; and the topsoil used for the deposit was a sandy loam which did not become compacted until after recovery had been made. There was no growth through the deposit of 6 inches depth.

BUCHLOE DACTYLOIDES

Buffalo grass *(Buchloe dactyloides)* propagates chiefly by stolons, although short underground stems are present (Fig. 16). Except for stolons, the habit of the plant resembles that of blue grama. An underground stem is formed by the short lateral growth of a bud before it turns upward to form a new culm. About 0.25 inch was added to the length of the horizontal stem each year. Seedlings developed rapidly
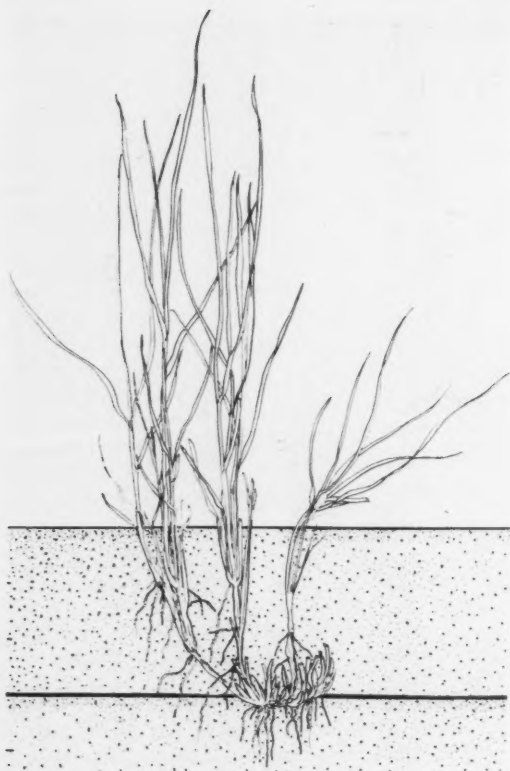
FIG. 15. Rhizomes of blue grama grass *(Bouteloua gracilis)* ascending through a deposit of soil 3 inches deep. The dead culms are near the original soil surface.

(Fig. 17). Plants in the greenhouse began to form stolons when only a month old, and under optimum conditions they elongated as much as 2.25 inches per day. Based upon a record of 6 stolons measured daily for one week, the average rate of growth was 1.2 inches per day. A seedling examined at the age of 63 days had 10 stolons, the longest of which was
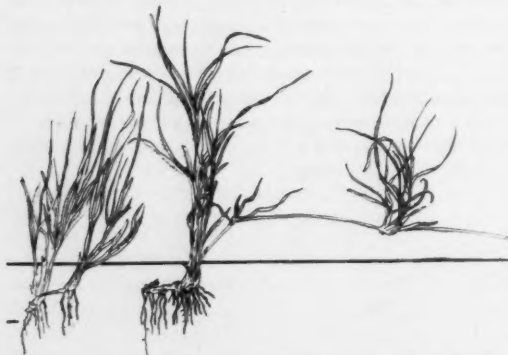
FIG. 16. Buffalo grass *(Buchloe dactyloides)* showing short rhizomes at about .5 inch depth and a stolon that has not yet rooted.
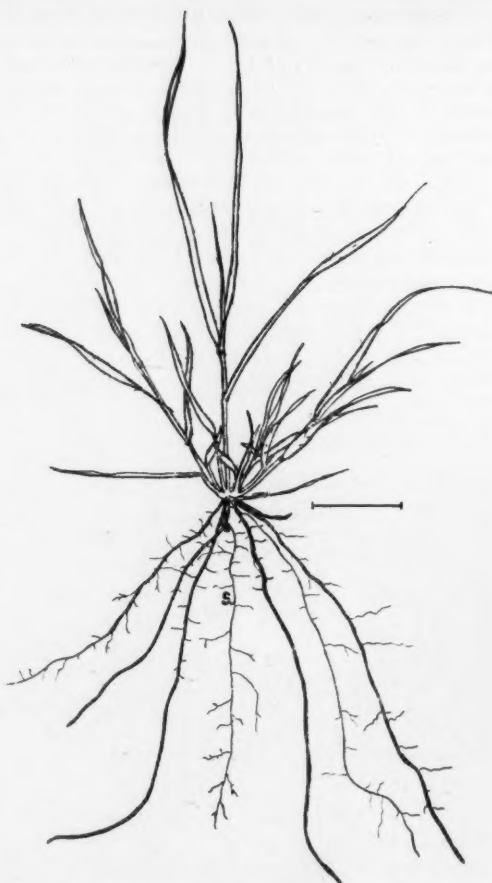
FIG. 17. Buffalo grass *(Buchloe dactyloides)* 23 days after emergence, showing seminal root (S) and secondary root system. Every tiller is a potential stolon. Length of scale, 1 inch.

24 inches and the shortest, 5. Forty-three of the nodes on these 10 stolons were rooted.

Stolons from the 9 sods set in the North Prairie Creek garden had covered the whole plot (about 81 sq. ft.) by July 1, 1938. During the first year the area increased from 36 sq. in. to 196 sq. ft., and by the end of the second year to 232.5 sq. ft. This is a total gain of 25.8 sq. ft. per sod. Since the soil was completely covered, except at the margins of the area occupied, by the summer of 1939, the new stolons could not become rooted but grew out over one another to form a mat of grass 7 inches thick (Fig. 3). When cut and air dried, early in September, one square meter taken from near the center of the mat weighed 2.1 pounds. A single acre covered with such a mat would produce 4.3 tons of forage. The weight of the grass from the entire area, including the thinner margins, was 28.1 pounds. Based upon this weight, the production was 2.6 tons per acre. This rivals the yields in a native bluestem meadow.

It is common knowledge that buffalo grass is poorly adapted for growth in sand. While stolons elongate rapidly above ground, they have considerable difficulty when buried under the soil. The grass is so short that drifting sand can quickly cover it. During the first summer, buffalo grass in the sand-hill garden was not noticeably hindered by erosion. A small increase in area of 4.7 sq. ft. was made. During the following winter and spring there was considerable wind action on the bare areas surrounding the sods. Sand was deposited in the centers of the sods and blown away from the margins. The cutting away of soil started by wind was continued by water when rains came. As a result, soil in the center of each sod was three inches higher than at its margin. The grass in the center died, but at the margin, where it was exposed or only lightly covered, buds developed and stolons were produced. Soon a green "fairy-ring" encircled each of the 9 mounds of sand (Fig. 18). The
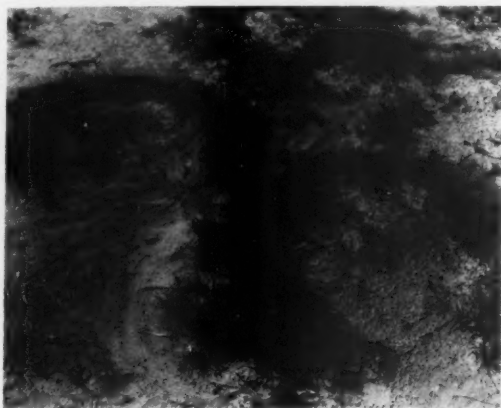
FIG. 18. "Fairy rings" of buffalo grass (*Buchloe dactyloides*) formed after the center of the sod had been destroyed by sand deposits.

increase in area per sod of 5.1 sq. ft. for the two years was about 0.2 as great as that on loam soil.

CALAMOVILFA LONGIFOLIA

Sand reed-grass (*Calamovilfa longifolia*) is a coarse plant found abundantly in sandy regions where it indicates a fairly high degree of stabilization. The ability of the rhizome to adjust itself to shifting soil levels was limited to a rather narrow range. From results obtained in the covered quadrats, the maximum depth of soil deposit through which recovery was made lies between 6 and 12 inches. In an area with a control count of 220 stems per sq. m., 41 recovered through a 6-inch deposit and none through 12 inches of sand. Examination showed that the ascent from the parent rhizome was more often inclined than vertical (Fig. 19).

Rhizomes of Calamovilfa were coarse, scaly, and well branched. New rhizomes began to develop in June. These had a diameter of 2 to 4 mm., and were sometimes flattened near the sharp terminal bud.
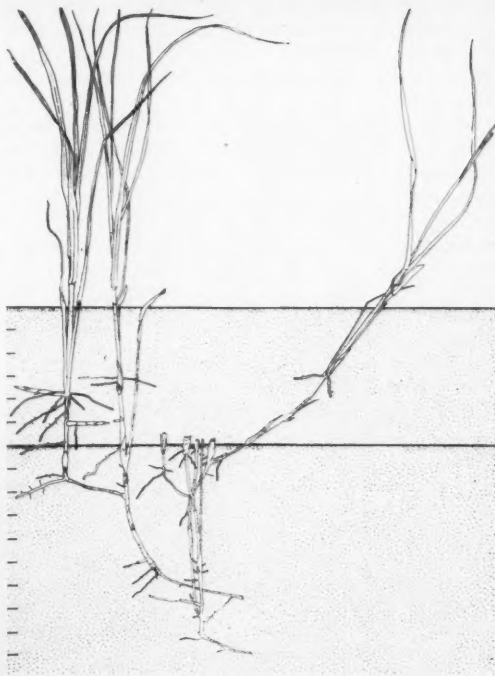
FIG. 19. Recovery of sand reed-grass (*Calamovilfa longifolia*) through a sand deposit, 6 inches deep. New horizontal rhizomes are at the normal level. The inclined ascent from the parent rhizomes was common.

Roots, which arose at the nodes, were often nearly as thick as the rhizomes. In natural grassland, the depth of the rhizomes ranged from 1.5 to 8 inches; in the loam garden it was from 5 to 11 inches, and in sand from 4 to 6 inches. The maximum length of new rhizomes was 13 inches and the average about 6 inches.

Culms were never closely aggregated and tended to be inclined rather than erect. Those at North Prairie Creek were about 6 feet tall but those in sand 4 feet. At the end of the summer of 1939, each plant at North Prairie Creek had an average of 39 culms included in an area of 1.1 sq. ft., while each in the sandy plot produced an average of 17 culms within 0.4 sq. ft. There were 2 new rhizomes per culm in loam and 3.4 in sand. Plants in loam produced 134 feet of rhizomes per sq. m. and those in sand, 101 feet. These were among the lowest productions recorded for grasses.

ELYMUS CANADENSIS

Rhizomes of nodding wild rye (*Elymus canadensis*) were short and tended to be inclined or vertical rather than horizontal. The average length was about an inch, and they were usually found in the upper 1.5 inches of soil. Plants grown in loose, sandy soil had rhizomes considerably longer and as deep as 5 inches. Scales of young rhizomes were much longer than the internodes. Consequently, several smaller scales were included within the larger ones. The average diameter

of a young rhizome was 2 mm. Plants growing in the gardens had produced one new rhizome for each culm by late September. Often new shoots developed late in summer and in autumn. Roots occurred only at the nodes.

No plants died in either garden. The average radial increase of clumps was 2 inches per year in loam and about 1.5 inches in sand. The total increase in area per plant was 0.5 sq. ft. in loam and 0.3 in sand. Rhizomes totaling 377 feet per sq. m. were produced in the loam garden. Those from plants grown in sand were not measured, but from the aggregation of stems and general condition of the bunches it was estimated that production was about the same.

A dense stand of seedlings appeared in the vicinity of the plot at North Prairie Creek in the early spring of 1939. The plants had fruited the previous summer and the heads were weighted down by drifting snow during winter. Since drainage was poor, the soil was wet when the snow melted. The mass of seedlings gave the impression of a turf as early as the first week in April. It was necessary to remove many of them from about the parent plants and from neighboring plots, but those in the paths were allowed to grow. They fruited late in June. By September, each surviving plant had produced an average of 12 stems, ranging from 38 to 40 inches in height. The parent plants were about 18 inches taller. It has been noted (Weaver and Fitzpatrick, 1934) that *Elymus canadensis* sometimes occurs in pure stands in areas subject to overflow. This acquisition of an area thus distributed may be facilitated by a relatively high rate of germination of seeds under conditions of high moisture and poor aeration very early in spring before other plants begin growth and by early maturation of seedlings.

PANICUM VIRGATUM

Sods of tall panic grass *(Panicum virgatum)* growing in sand made greater gains than those in the heavier soils of the bottom lands. This was true for plants examined in natural grassland as well as for those in the gardens. The most robust rhizomes, which grew in dune sand on an elevation considerably above an area occupied by big bluestem, were taken from a family measuring 10 by 26 feet. Here the well-branched rhizomes were from 1.5 to 3.5 inches deep. The average advance between living culms and those produced the previous year was 3 inches and the maximum distance was 5 inches. Internodes were short, varying from 3 to 5 mm. The diameter of the rhizomes near the bases of the culms was about 7 mm.; elsewhere it was about 3 mm. New rhizomes, covered with scales 10 to 15 mm. long, appeared early in June. The scales were decayed on old rhizomes leaving ragged margins where remnants of veins still projected from the nodes. Roots were nodal and more numerous near bases of culms (Fig. 20). Plants taken from the margin of a lowland meadow showed the same general habits, but here the maximum advance was 3 inches and the average about 2.
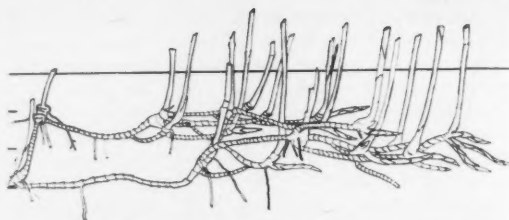
FIG. 20. Rhizomes of tall panic grass *(Panicum virgatum)*, 1 to 3 inches deep, grown in dune sand. New rhizomes had attained a length of 1.5 inches early in July.

These plants were growing in competition with slough grass. Those growing in other localities showed still smaller gains.

Plants in the sand-hill garden made an average gain in area of 1.1 sq. ft. for the 2 years. In 1939, the clumps of sod averaged 14.5 inches in diameter, and produced 170 culms with an average of 2.3 new rhizomes per culm. These ranged from mere buds to stems 2 inches long. Based on the total length of all rhizomes in a clump, it was computed that 344 ft. per sq. m. had developed. At North Prairie Creek, each plant gained about 0.9 sq. ft. during the two years. Culms were 18 inches taller and more closely aggregated. Sods with average basal diameters of 13 inches produced an average of 205 culms each (Fig. 21). There were only 1.4 new rhizomes per culm. The size of these was about the same as those grown in sand. Accompanying the curtailment of the number of new rhizomes, production was reduced to 306 ft. per sq. m.

FIG. 21. Two-year-old clump of tall panic grass *(Panicum virgatum)* grown in loam soil. It has a basal diameter of 13 inches and is about 4.5 feet tall.

FIG. 24. Rhizomes of reed canary grass *(Phalaris arundinacea)* in upper two inches of soil. Roots are distributed on both nodes and internodes. Scale in inches.

from 1 to 5 inches. The average increase in area per sod for the two years was 1.7 sq. ft. in loam and 0.6 sq. ft. in sand. Each culm in the loam soil produced an average of 4.2 new rhizomes. New rhizomes developed and produced new shoots throughout the summer. Kirehner, Loew, and Schroter (1909) found that this species, growing in central Europe, produced from 3 to 5 generations of sprouts in a year. Occasionally culms became inclined, and if the topsoil was moist, these rooted at the nodes and produced new upright stems. Thus, this grass may gain territory either by rhizomes or by stolons.

POA PRATENSIS

Sods of Kentucky bluegrass *(Poa pratensis)* transplanted to sandy soil without protective cover soon succumbed to high temperatures and extreme aridity. Those placed in loam became established and increased their areas by an average of 3.9 sq. ft. during the two years. Approximately four slender, branched rhizomes arose from each culm. These turned upward to form other culms 4 to 12 inches from the parent. New rhizomes had a diameter of 1.5 mm. but the old ones were only 1 mm. thick. The difference probably was due to the concentration of food reserves in young rhizomes, which were depleted when new culms developed. Rhizomes often died soon after the new culms became established. Bluegrass sod is compact because of numerous very fine roots which grow from the nodes. Nodes were from 0.5 to 1 inch apart but scales were slightly longer. These became broken along the veins and soon disintegrated. All rhizomes were found in the upper 3 inches of soil (Fig. 25). Rhizomes removed from a square-meter sod had a total length of 583 feet. This production in loam soil was exceeded only by wheat grass. Seven stems of *Poa pratensis* grew through the 3 inches of soil deposit which covered a quadrat of *Andropogon furcatus.*

Seedlings were found near the experimental plot. After a season's growth, one plant had a basal diameter of 1.5 inches and had produced 30 rhizomes with a radial spread of 5.5 inches.

FIG. 22. Seedling of tall panic grass *(Panicum virgatum)* producing tillers when only 27 days old. Length of scale, 1 inch.

FIG. 23. Seedling of reed canary grass *(Phalaris arundinacea)* with several tillers. Age, 27 days. Length of scale, 1 inch.

Seedlings of *Panicum virgatum* grown in the greenhouse, gave rise to tillers within 27 days (Fig. 22). Short rhizomes were found after 63 days of growth. They were numerous and well developed by the end of 100 days.

PHALARIS ARUNDINACEA

Seedlings of reed canary grass *(Phalaris arundinacea)* grown under favorable conditions began to tiller at an early age (Fig. 23). They formed rhizomes before the plants were 2 months old. The rhizomes grew out from beneath the clump and were directed downward for some distance before turning upward to form culms. The lower part of the loops thus formed were sometimes an inch deeper than the ends. An abundance of roots, attached at both nodes and internodes, combined with the mass of well branched rhizomes, formed a sod that was almost impenetrable. The scales were slightly longer than the internodes and pink when young. Internodes varied in length from 3 to 17 mm. Plants growing in wet places produced new rhizomes with a maximum length of 4 inches. These were in the upper 2 inches of soil (Fig. 24). In the loam garden, the maximum length attained was 2.5 inches and the average, 1.8. The average length in sand was only 1 inch. The total length of rhizomes in a square meter of loam was 383 feet. The range in depth in both gardens was

FIG. 25. Kentucky bluegrass *(Poa pratensis)* showing the slender rhizomes which often perish soon after new stems are well established. They were confined to the upper 3 inches of soil. Scale in inches.

SORGHASTRUM NUTANS

Development of tillers and rhizomes in seedlings of Indian grass *(Sorghastrum nutans)* was somewhat retarded. Those grown in the greenhouse produced no tillers until the fourth week, nearly 7 days later than other species of tall grass. No rhizomes were found on plants 14 weeks old.

Mature plants began to form new rhizomes in August. They were sparingly branched and usually about 1 to 2 inches long, but a maximum length of 4 inches was attained in moist, sandy soil. Frequently rhizomes curved downward from the parent stem for a short distance and then turned abruptly upward. The long, pointed, terminal bud was near the soil surface while the lower portion of the loop was about 2 inches deep. Scales were two to three times the length of the internodes. Roots were produced at both nodes and internodes (Fig. 5).

Only four plants survived in each of the experimental gardens. All were thrifty and produced flower stalks as much as 8 mm. in diameter the first season. The average yearly lateral spread in both gardens was 2 inches, and average increase in area per sod for the two years was 0.5 sq. ft. In loam, there were 58 culms per clump and 191 feet of rhizomes per square meter; in sand there were 76 culms and 284 feet of rhizomes.

SPARTINA PECTINATA

The coarse, pale yellow rhizomes of slough grass *(Spartina pectinata)* are sheathed, when young, with hard pointed scales which are somewhat longer than the internodes. These are often of su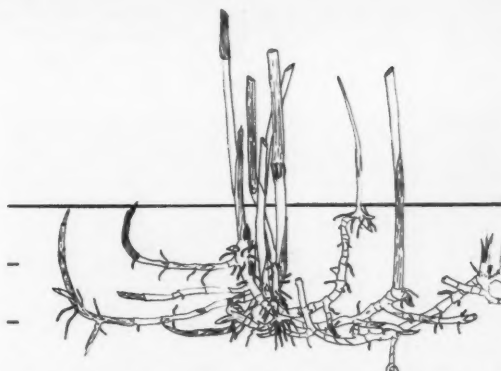ch a texture that the rhizome appears as if it had been dipped in clear lacquer. The terminal buds are rigid and sharp pointed. New rhizomes, 5 mm. or more in diameter, began to form early in summer and by autumn attained average lengths of 10 to 12 inches. The longest one excavated was 20 inches. The depth range was considerable. Some were found as deep as 10 inches in the bed of an intermittent stream. They evidently had been covered by soil which had been deposited by water (Fig. 26). New rhizomes attached to the old ones were only 6 inches deep. In the garden at North Prairie Creek, the depth range

was from 1 to 7 inches and in the sand hills, from 4 to 8 inches. Roots were distributed on both nodes and internodes. Plants excavated by Weaver (1920) showed similar ranges in depth and size of rhizomes.

The habitat at North Prairie Creek was favorable for production of slough grass. Foliage was 4.5 feet and flowering stems were 6.5 feet tall. The average gain per plant was 4.3 sq. ft. in two years, while in sand the gain was 3.1 sq. ft. The aggregation of stems was 472 per sq. m. as compared with 328 in sand. Photosynthetic activity was sufficient to produce an average of 3 new rhizomes per stem in loam and 2 in sand. The production of rhizomes in feet per square meter is usually low for species with coarse underground parts. Slough grass is no exception as is shown by 163 and 127 feet developed in loam and sand, respectively.

Adjustments to new soil levels, resulting from deposits of mud or dust are readily made if the change is no greater than 6 inches. In an area with a sample count of 270 stems per sq. m., 176 stems came through a 3-inch soil deposit and 57 through a deposit of 6 inches. None emerged through 12 inches of soil.

EXPERIMENTS AND RESULTS WITH FORBS

APOCYNUM SIBIRICUM

Clasping-leaved dogbane *(Apocynum sibiricum)* was an important constituent of grassland, especially in lowland prairie before the breaking of the sod. Although conspicuous, competition with the grasses was not great, since an individual produced little shade, and the stems were widely spaced. *Apocynum sibiricum* was not destroyed, as were nearly all native species, by the conversion of prairies into cultivated fields. Crops were poorer competitors, and Apocynum often was able both to increase its area and to become closely aggregated. Norris (1939) has shown that it is a weed of great importance in fields of eastern Nebraska. It was not associated with one special crop, but regardless of methods of tillage seemed equally important in all.

Vegetative propagation is accomplished by horizontal roots which bear adventitious buds, or by the development of buds at the nodes of the vertical rhizomes. In general, the underground system of
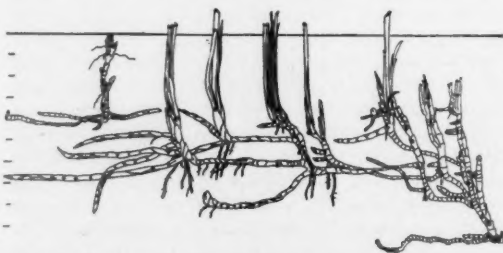
FIG. 26. Rhizome of slough grass *(Spartina pectinata)*. The older portion, A, which is an extension of B, was covered with soil deposited by an intermittent stream. Maximum depth was 10 inches.

Apocynum sibiricum is comparable with those of *A. androsaemifolium*, described by Weaver (1919), and Canada thistle *(Cirsium arvense)*, described by Hayden (1934). The perennial roots are of two types: thick, branched, horional ones, whose chief function is the production of new ascending shoots, and more slender, well-branched, vertical, absorbing roots. The horizontal roots varied considerably in depth. Ascending shoots arose from roots as shallow as 5 inches and as deep as 16. Spacing of stems was also variable. The distance between shoots was sometimes 5 feet but more often only 6 to 12 inches. Sources of new shoots, so deeply situated, are rarely disturbed by plowing. Photosynthesis, moreover, is only temporarily interrupted with ordinary cultural practices, since new shoots appear throughout the growing season.

The vertical rhizomes were a centimeter or more in diameter. Nodes, poorly defined by external markings, were from 1 to 2 inches apart. The two, small, dark brown, papery scales found at each node, were early deciduous. Buds often developed near the surface and produced aggregations of 2 or 3 shoots. Fine absorbing roots arose from various portions of the rhizome as well as from the horizontal roots.

Six plants at North Prairie Creek, during two seasons, gained about 80 sq. ft. per individual. The single plant which survived in sand made an increase of 232 sq. ft. This does not necessarily indicate that the total spread of a plant was greater in sand. Many of the propagating roots from each parent in loam advanced into territory already partially occupied by another individual until, in the older portion of the plot, a meshwork of the roots of all six plants was formed. The increase was the greatest of any species in either garden. In loam, there were 394 stalks ranging in height from 28 inches at the margins of the plot to 57 inches near the center. There was no defoliation of marginal stalks, but leaves had fallen on the basal 12 inches of the stems where shade was more dense. In sand there were about one-seventh as many stalks and they were only three-fifths as tall.

ARTEMISIA GNAPHALODES

Prairie sage *(Artemisia gnaphalodes)* is often densely aggregated in pure stands 2 to 3 meters in diameter. Examination of such a family showed that it had originated from a single parent and that all the stalks were connected by underground stems which often persist for several years. At the periphery, each stalk was producing from its thickened base 10 to 12 tender, new rhizomes less than a millimeter thick. These became increasingly thickened with age until near the center of the community they were 10 mm. or more in diameter. Branches were so interlaced that a firm meshwork was formed in the upper two inches of soil. Roots were distributed on both nodes and internodes and firmly anchored the mat.

The percentage of survival was so low during the first winter that it was necessary to transplant a new lot of this sage in both gardens. As a consequence, the gain in area was almost nil the first summer. By the end of the second year, each plant occupied an average area of 11 sq. ft. in loam and 4.9 in sand. At North Prairie Creek, the stalks were nearly 3 feet tall by the end of the summer (Fig. 27). An average

FIG. 27. Prairie sage *(Artemisia gnaphalodes)* at North Prairie Creek. These plants produced 534 feet of rhizomes per square meter. *Solidago glaberrima* is shown in the foreground.

of 25 new rhizomes with a mean length of 7 inches was produced from each of these stalks. The longest were 31 inches. Average height of stalks in sand was only one-half as great and less than one new rhizome was produced from each. On the other hand, this plot had produced almost 9 times the number of stalks in only one-third as much area as the plants in loam. It appears that a greater number of buds developed directly into shoots with a resulting decrease in spread and closer aggregation of stalks. The rhizome production of 534 ft. per sq. m. at North Prarie Creek was the greatest recorded for any forb. Here the range in depth was from 1 to 5.5 inches.

Considerable ability to grow through soil deposits was shown. Fifty-eight stems were found growing on the 3-inch deposit and 5 on the 6-inch. Rhizomes ascended vertically from old levels to produce shoots the second summer. New horizontal rhizomes developed at the normal level in both quadrats (Fig. 28).

ASTER MULTIFLORUS

Many-flowered aster *(Aster multiflorus)* was formerly widely distributed as isolated individuals or small clumps and ranked as one of the most important upland forbs in the prairie (Weaver and Fitzpatrick, 1934). After the death of competing species by drought, communities of aster, 6 to 8 feet in diameter, became common. A contributing factor to this alarming increase was an efficient system of underground stems. Rhizomes may function as food reservoirs and initiate new stems over a period of several years (Fig. 29). Plants grown at North Prairie Creek produced an average of 6.7 new rhizomes per green shoot, a number surpassed only by prairie sage. Maximum length was 17 inches and the average, 6
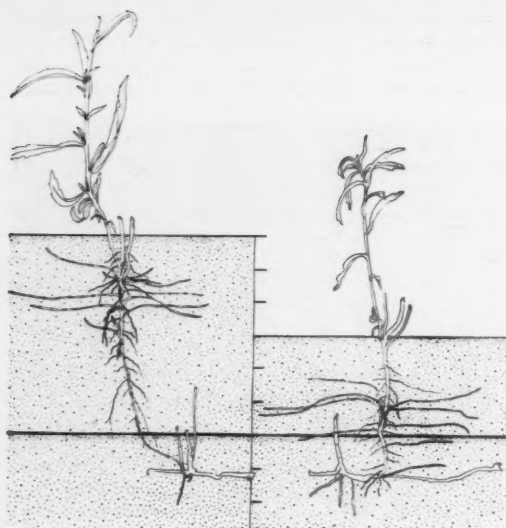
FIG. 28. Growth of prairie sage *(Artemisia gnaphalodes)* through soil deposits of 6 inches (left) and 3 inches (right). Numerous, young, horizontal rhizomes developed at normal levels.

inches. Plants growing in competition with other species produced rhizomes which averaged only 4 inches long. Old rhizomes were dark brown, well branched, and had diameters of 4 mm. or more. Those recently produced varied from light brown near the origin to white at the growing point. Diameter was about half that of older rhizomes. Roots were attached either at the nodes or the internodes. No rhizomes deeper than 2 inches were found in field investigations, but a 6-inch maximum was recorded for those in the garden at North Prairie Creek. The total length of rhizomes in a square meter in loam was about five-sixths as great as that of the bluestems, panic grass, and side-oats grama. Shively and Weaver (1939) found that volume and dry weight of subterrean parts (including roots) to a depth of 4 inches
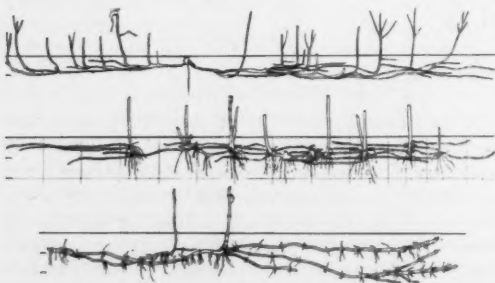
FIGS. 29, 30, and 31. The upper figure (29) shows the rhizomes of many-flowered aster *(Aster multiflorus)* which are .5 to 1.5 inches deep. Those near the center are 3 years old. Scale in inches. Fig. 30 (center). Rhizomes of smooth goldenrod *(Solidago glaberrima)* .5 to 1.5 inches deep. Fig. 31 (lower). Two generations of rhizomes of fringed loosestrife *(Steironema ciliatum)*. Depth, .5 to 2.5 inches.

"were only a small part of that of the underground parts of the grasses which they had replaced." The increase in area per plant was 0.9 sq. ft. Plants were unable to survive in the sand.

The percentage of recovery through layers of soil was lower for the aster than for either prairie sage or smooth goldenrod. Seven stems grew through 3 inches and 8 through 6 inches of soil. New rhizomes ascended almost vertically from the old ones (Fig. 32).
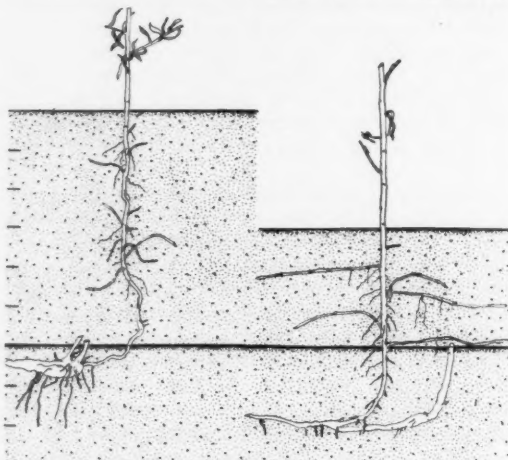
FIG. 32. Vertical ascent of many-flowered aster *(Aster multiflorus)* through soil deposits of 6 and 3 inches depth.

ASTER SALICIFOLIUS

Willow-leaved aster *(Aster salicifolius)* became well established in the lowland garden but was so continuously injured by some rodent eating the shoots that little growth occurred the first summer. Rootstocks were produced, however, since the 533 stalks which appeared the second spring occupied an area of 96.9 sq. ft. By autumn, the stems were 4.5 feet tall and 1.5 cm. in diameter. Those in the center of the plot had lost their leaves near the base but the others were not defoliated. Upon removal of soil, a prolific growth of new rhizomes, numbering 5.9 per stalk, was revealed. These extended from 2 to 3 feet beyond the area occupied by the aerial stems. They were about 3 mm. in diameter and 1 to 5 inches deep. The total length, including both old and new rhizomes, was 330 ft. per sq. m. This is double the production found for *Spartina pectinata* in the same garden. Roots appeared at the nodes and internodes. There were but two very dwarfed plants in the sandhill garden at the close of the second year. Together they produced 20 rhizomes with a total length of 153 inches.

POLYGONUM MUHLENBERGII

Tanweed, or smartweed *(Polygonum muhlenbergii)* occurs in fields of eastern Nebraska and is especially associated with wheat (Norris, 1939). It propagates by means of extensive perennial rhizomes. The brown color of the older portions fades to a cream tinged

with pink near the growing tip. The dark brown, papery scales are about 0.5 inch long. Diameter of rhizomes varied from 4 to 12 mm. The nodes were somewhat swollen but this characteristic was not so pronounced as in the aerial stems. Internodes were from 0.5 to 5 inches long. Numerous, finely branched roots and some heavy ones, which penetrated deeply, appeared at the nodes. The depth of rhizomes under normal conditions varied from 6 to 15 inches with the majority near the 15-inch level (Fig. 33). Those
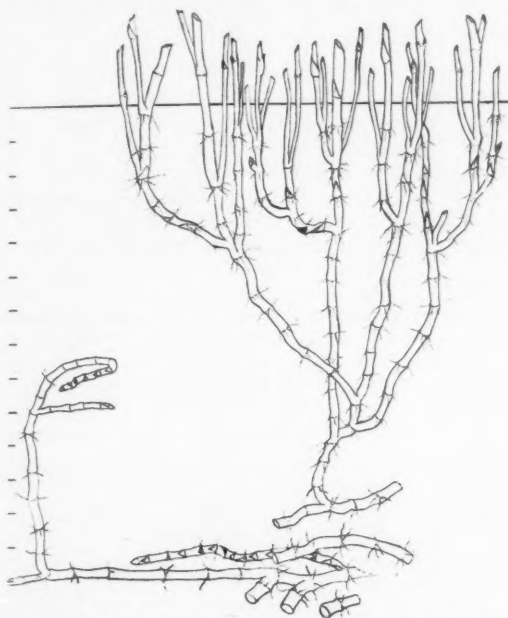
Fig. 33. Robust rhizomes of tanweed *(Polygonum muhlenbergii)* more than 14 inches deep. This is a common weed, especially in fields of wheat.

planted in the loam garden attained a maximum depth of 12 inches, but those in sand were 18 inches deep. Such rhizomes would never be disturbed by ordinary tillage operations. Branches which gave rise to aerial stems ascended almost vertically. Each vertical rhizome branched 2 to 3 inches below the soil surface and produced an average of 6 stems. Only about two-thirds as many new rhizomes as aerial stems were developed each year, but each rhizome branched many times so that the increase in aerial stems the following year was considerable. The average length of rhizomes produced in one season in the North Prairie Creek garden was 47 inches (maximum 59) as compared with 30 inches in sand. Total production of rhizomes in loam soil was 20 ft. per sq. m.; in sandy soil it was only 2 feet less. During the two years, average gains of 31.4 sq. ft. were made by plants growing in loam and 1.8 sq. ft. by those in sand.

Experiments showed that the rhizomes of *Polygonum muhlenbergii* can withstand considerable periods of desiccation. This varied with the stage of development of the plant from which the rhizomes

were taken. Those from plants not yet developing shoots showed the greatest resistance. Among 24 rhizomes exposed to the air for 44 hours, only 1 failed to grow. Sixty-eight hours was the maximum period of exposure after which growth was obtained. Of the lot taken from plants with shoots 6 inches high, none grew after more than 46 hours exposure to air. The lethal length of exposure for rhizomes taken from plants 2 feet tall was between 24 and 46 hours. The time required for sprouts to appear above the soil varied directly with the length of the period of exposure. For the first lot, the controls and those dr'ed 18 hours produced shoots in 5 days. Those exposed 44 hours were in the soil 11 days before sprouts appeared. When dried 68 hours, it required 20 days. Similar progressions were noted in the two remaining lots. There was no evidence of decay in any of the rhizomes which failed to sprout. These experiments are merely indicative since the number of rhizomes tested was small (Table 2).

TABLE 2. Viability of rhizomes of *Polygonum muhlenbergii* after different periods of exposure to air.

Period of exposure (hours)	Length of rhizomes (inches)	Number planted	Per cent which grew
Excavated April 6			
0	3 to 6	24	100
18	3 to 6	24	1C0
44	3 to 6	24	96
68	3 to 6	24	4
115	3 to 6	26	0
Excavated May 8			
0	6	12	100
22	6	12	100
46	6	12	9
52	6	12	0
70	6	24	0
Excavated June 18			
0	6	12	83
24	6	12	50
46	6	24	0
74	6	24	0

SOLIDAGO ALTISSIMA

Tall goldenrod *(Solidago altissima)* is a robust species commonly found in wet grassland. It propagates by coarse rhizomes which may develop from buds formed at the nodes of other underground stems or from buds developed adventitiously on the roots. The latter habit seemed more pronounced when the plants were growing in habitats which they did not normally occupy. Several horizontal roots, knotted with numerous buds, advanced from each plant in the sand-hill garden. Some of these were 30 inches long. Rosettes more than 6 inches distant were always connected to the parent clump by these roots. This habit was not conspicuous at North Prairie Creek.

A typical system of underground stems is portrayed in the following description of a plant growing near

the bank of a small stream. The previous year one central stalk, now dead, had matured three rhizomes, averaging 8 inches in length. The ends of these had turned upward to produce the stalks which were alive at the time of examination. These old rhizomes were pale brown in color, 5 mm. thick, and about 3 inches deep. As many as 12 buds near the bases of the shoots were developing into new rhizomes some of which were 12 inches long. The new rhizomes varied in color from white to bright pink with deep brown, alternate scales. The width of a scale at the base was about one-half the circumference of the rhizome. Roots were more abundant at the bases of the stalks and were attached either at nodes or internodes (Fig. 34).

FIG. 34. Top view of rhizome system of a plant of tall goldenrod *(Solidago altissima)*. Distance between dead stalk (A) and living stalk (B) is 11 inches. Roots were aggregated near the bases of the erect stems.

The aerial stems of the plants growing at North Prarie Creek showed a marked response to different degrees of competition. In the summer of 1938 there were 27 in the plot. These were grouped into 9 clumps each with a basal diameter of 3 inches. Stems attained a diameter of three-fourths inch and a height of about 4.5 feet. They were well branched and the spread was sufficient to produce a complete foliage cover over the whole plot. In 1939, there were 319 stems in an area 10.5 by 8.5 feet. These stems had only half the diameter and fewer branches but were 6 inches taller than those of the preceding year. Foliage had been lost to a height of 40 inches. The

rhizomes were longer in 1938, and a distance of 18 inches was recorded between dead and living stems. The maximum length of rhizomes produced in 1939 was 13 inches. These responses may have been conditioned by differences in distribution of rainfall during the two seasons.

Plants made an average increase in area of 9.9 sq. ft. at North Prairie Creek and 2.8 in the sand hills during two years. Stems produced an average of 5.5 new rhizomes in loam soil and 1.8 in sand. Length of rhizomes per square meter was low, 89 feet in the loam and 12 in sand.

SOLIDAGO GLABERRIMA

A study of the system of underground stems of smooth goldenrod *(Solidago glaberrima)* clearly reveals one important reason for the relative abundance of this forb in the prairies when grass population is normal and its successful invasion into bare areas when the cover is broken by overgrazing or drought. Lengths of new rhizomes were about the same as those of *Aster multiflorus* (Fig. 30). The longest was 17 inches, average diameter was about 2.5 mm., and average production of rhizomes was about 6 per stem. In pure, dense stands there were 600 to 700 stems per square meter. Not all of the rhizomes originated from stem tissue; adventitious buds producing slender rhizomes frequently arose from roots. Often these buds were clustered so closely on the upper surfaces of a root that a condition of proliferation was approached. Greater distances were gained by this method of propagation. Occasionally rosettes were found two feet distant from the parent clump. They were always produced as offshoots from horizontal roots. The first rhizomes formed by seedlings were also root offshoots. The greater number of roots were near the thickened base of the shoot. They were not confined to the nodes but were found on the internodes as well. The production of 340 feet of rhizomes per square meter in loam compares favorably with that of most of the grasses. In sandy soil production of rhizomes by grasses was much greater than by forbs. The increase in area of 11.5 sq. ft. per plant in loam was twice that in sand.

Plants in quadrats covered with 3 and 6 inches of soil showed remarkable recovery at the end of a year, 208 stems growing through 3 inches of soil, and 430 through 6 inches. Rhizomes ascended vertically from the original levels to produce shoots the second season. New horizontal rhizomes were developing at normal depths of 1 to 3 inches when examination was made at the end of the year (Fig. 35).

OTHER FORBS

Solidago rigida or stiff goldenrod growing in prairie forms compact clumps composed of several rigid, leafy stems. They arise from a thick, fleshy crown which may spread radially 1 to 2 inches a year. After functioning for two or more years, the crown may die at the center and thus produce a small bare area surrounded by a ring of stems. Like the other goldenrods studied, propagation is also by means of adven-

FIG. 35. Vertical ascent of rhizomes of *Solidago glaberrima* through 6 inches (left) and 3 inches (right) of soil deposit.

titious buds produced from horizontal roots. It is probable that this method has made possible the rapid spread of stiff goldenrod under conditions of severe grazing. Three clumps survived in the sand-hill garden. During the two years they made an average increase in area of only 0.25 sq. ft.

Urtica gracilis, the slender nettle, is a coarse perennial with both aerial parts and extensive rhizomes armed with stinging hairs. The ability to sting is much reduced in the latter since the hairs fail to harden in the moist environment of the soil. The angular rhizomes, usually about 6 mm. thick, had a depth range of 1 to 8 inches. Roots penetrated the soil from the nodes which occurred at intervals of 1 to 4 inches. In loam, stems were 5 feet tall and nearly 1.5 cm. thick. A hailstorm in late June had removed many leaves and during the July drought the stems were defoliated to a height of 4 feet. Thereafter, axillary buds developed into branches and leaves nearly to the bases of the stalks. A total of 768 stems, spaced at intervals of 4 to 12 inches, were produced in 1939. The ratio between new rhizomes and stalks was 7 to 2. The maximum length of new rhizomes was 44 inches and average length 19. Rhizomes taken from an area of one square meter totaled 113 feet in length. Those planted with the original stems were still alive. Average gain in area for each of the nine was 27.7 sq. ft.

In the sandy plot, 7 weak plants survived the first year. Stems were less than a foot tall. Several sprouts appeared the following spring, but all were dead by September.

Glycyrrhiza lepidota, wild licorice, is a legume found commonly in lowlands. Its branched rhizomes function for many years. They were found in the soil between depths of 1.5 to 12 inches. New rhizomes began growth early in summer and attained a length of 6 feet by mid-August. The diameter varied between 2 and 12 mm. Alternate scales resembling the rhizomes in color extended only about 6 mm. beyond the node and were much shorter than the internodes. The white color of young growing regions shaded into brown. The corky outer layer of the older portions was broken and traversed with a network of light brown lines. Roots were found at the nodes. Those located near green stalks became very fleshy.

Steironema ciliatum, the fringed loosestrife, is a lowland species that was planted only in loam. All survived the first winter, but 3 plants died the first summer and 2 the second. The remaining 4 made considerable advance. The average increase in area per plant was 6.4 sq. ft. The 88 stems produced 352 new rhizomes, about 4 per stem. The average diameter was 2.5 mm. and the length, 6.2 inches. The maximum length was 14 inches, and 81 feet of rhizomes were taken from a square meter. Rhizomes were well branched and occurred from near the surface to a depth of 5 inches. They were brownish-pink in color and pubescent when young. Internodes were from 1 to 1.5 inches long; roots occurred only at the nodes. Scales and buds are opposite in arrangement. The span of life of a rhizome was slightly more than a year (Fig. 31).

DISCUSSION

A study of data from 19 quadrats shows an unexpected ability of several native perennial grasses and forbs to make adjustments and maintain viability under soil deposits of varying depths (Table 3). Of the grasses included in the experiment, *Agropyron smithii* grew through the deepest deposit. Even after a year, parent rhizomes were alive and shoots ascended through 12 inches of soil. Many parent rhizomes extended beyond the boundaries of the quadrats and food may have been supplied by stems growing in the light. *Andropogon furcatus* was the only species that showed a high death rate of parent rhizomes. It would seem that species with robust rhizomes such as those possessed by *Calamovilfa longifolia* and *Spartina pectinata* would have recovered through deposits of greater depths. The annual extension of their rhizomes, however, is usually less than 12 inches. Response of *Solidago glaberrima* indicates that recovery through deeper deposits may be possible. The unusual recovery of *Bouteloua gracilis* was undoubtedly influenced by an abundance of soil air and optimum soil moisture.

Species exemplifying several modes of vegetative propagation are included in this study. *Buchloe dactyloides* is stoloniferous; *Apocynum sibiricum* advances by horizontal roots which produce adventitious buds; other species propagate by rhizomes. Several combinations of these methods are also represented. In addition to stolons, Buchloe possesses very short

TABLE 3. Number of stems per square meter that had grown through 3 to 12 inches of soil one year after burial.

Species	Depth of deposit in inches			
	0	3	6	12
Andropogon furcatus	570	89	0	0
Artemisia gnaphalodes	716	58	5	—
Aster multiflorus	345	7	8	—
Agropyron smithii	658	65	55	2.5
Bouteloua gracilis (bunches)	8	22	0	—
Calamovilfa longifolia	220	—	41	0
Solidago glaberrima	655	208	430	—
Spartina pectinata	270	176	57	0

TABLE 4. Behavior of aerial stems and rhizomes of plants grown in loam (numbers following name) and in sand (numbers in italics).

Species	Percentage survival	Ave. No. stems per plant	Ave. No. new rhizomes per stem	Max. depth rhizomes, in.	Ave. length new rhizomes, in.	Max. length new rhizomes, in.	Ave. increase in area, sq. ft.	Total length rhizomes, ft. per sq. m.
Agropyron smithii	100	¹830	1.0	5.0	52.0	80.0	53.8	619
		106	*1.0*	*5.0*	*10.0*	*40.0*	*12.7*	*48*
Andropogon furcatus	89	85	5.0	3.0	1.5	2.0	0.5	319
	100	*86*		*2.0*			*0.4*	
Andropogon scoparius	67	317		1.5	0.7	1.5	0.6	309
	100	*397*		*1.0*			*0.5*	
Bouteloua curtipendula	78	119	0.7	2.0	1.0	2.0	0.44	331
	78	*277*	*0.7*	*2.0*	*1.0*	*2.0*	*0.43*	
Bouteloua gracilis	89	221		0.5			0.4	
	56	*266*					*0.6*	
Buchloe dactyloides	100			0.5			25.8	
	100						*5.1*	
Calamovilfa longifolia	89	39	2.0	11.0	6.7	13.0	1.1	134
	67	*17*	*3.4*	*6.0*	*5.5*	*12.0*	*0.4*	*101*
Elymus canadensis	100	115	1.6	5.0	1.0		0.5	377
	100	*62*	*1.0*	*5.0*			*0.3*	
Panicum virgatum	100	205	1.4	1.0	1.0	2.0	0.9	306
	100	*170*	*2.3*	*2.0*	*1.0*	*2.0*	*1.1*	*344*
Phalaris arundinacea	100	180	4.2	5.0	1.8	2.5	1.7	383
	44	*96*		*5.0*	*1.0*		*0.6*	
Poa pratensis	100		4.0	2.5	6.0	9.0	3.9	583
	0	*0*	*0*	*0*	*0*	*0*	*0*	*0*
Sorghastrum nutans	44	58	1.0	2.0	1.0	3.0	0.5	191
	44	*76*	*1.0*	*2.0*	*1.5*	*2.0*	*0.5*	*284*
Spartina pectinata	100	187	3.0	7.0	12.0	19.0	4.3	163
	67	*96*	*2.0*	*8.0*	*9.0*	*14.0*	*3.1*	*127*
Artemisia gnaphalodes	100	22	25.0	5.5	7.0	31.0	11.0	534
	78	*128*	*0.8*	*4.0*	*7.0*	*9.0*	*4.9*	*109*
Apocynum sibiricum	67	66					79.7	
	11	*56*					*232.4*	
Aster multiflorus	100	40	6.7	6.0	6.0	17.0	0.9	268
	11	*3*	*0*		*0*	*0*	*0*	*1*
Aster salicifolius	78	76	5.9	5.0	13.5	36.0	13.8	330
	22	*2*	*5.0*	*3.5*	*7.5*	*15.0*	*0*	*24*
Polygonum muhlenbergii	78	40	0.7	12.0	47.0	59.0	31.4	20
	89	*23*	*0.5*	*18.0*	*30.0*	*40.0*	*1.8*	*18*
Solidago altissima	100	35	5.5	4.0	3.0	18.0	9.9	89
	89	*46*	*1.8*	*4.0*	*1.0*	*4.0*	*2.75*	*12*
Solidago glaberrima	100	139	5.9	3.0	6.0	17.0	11.5	340
	100	*76*	*3.2*	*5.0*	*6.0*	*10.0*	*5.75*	*95*
Solidago rigida	*33*	*17*					*0.25*	
Steironema ciliatum	44	22	4.0	5.0	6.2	14.0	6.4	81
Urtica gracilis	100	85	3.5	7.0	19.0	44.0	27.7	113
	0	*0*	*0*	*0*	*0*	*0*	*0*	*0*

¹Stems per square meter.

rhizomes. Phalaris may develop stolons when soil is wet and light values are low. Most of the grasses combine tillering with the rhizome habit. The goldenrods often advance by horizontal roots as well as by rhizomes. The greatest gains were made when the horizontal root method was employed and the smallest when rhizomes were short and tillering was the chief means of vegetative increase (Table 4). Any species with a pronounced stoloniferous habit ranks high in its ability to invade bare areas such as were provided in the experimental gardens. *Buchloe dactyloides* was one of the five species which led in gaining area. Species with rhizomes differed greatly in ability to increase their area. Those which quickly produced numerous, long, well-branched rhizomes made the greatest gains. Efficiency was also conditioned by the time of initiation and the duration of the growth period and by the span of life of the rhizome. Radial gains were relatively small when the main period of elongation occurred late in fall or early in spring. Growth then depended on food stored the summer before. If elongation was continuous throughout a growing season, usually greater increases were made. Species whose rhizomes were long-lived more often retained invaded areas than those whose rhizomes lived just long enough to produce new shoots.

Rhizome production within a species was usually correlated with production of tops. When rhizome production of those species included in experimental gardens was compared with aggregation and size of stems, the correlation held true for all species except *Panicum virgatum, Artemisia gnaphalodes,* and *Solidago altissima.* Species with coarse rhizomes ordinarily produced fewer feet per given area than did species with slender rhizomes. *Polygonum muhlenbergii,* with rhizomes 7.5 mm. in diameter, produced in loam soil only 20 ft. per sq. m. or nearly 60 feet less than any other species. *Agropyron smithii, Andropogon scoparius, Poa pratensis,* and *Artemisia gnaphalodes* all possessed rhizomes with an average diameter of less than 2 mm. In loam soil, *Agropyron smithii* produced more than 600 ft. per sq. m., *Poa pratensis* and *Artemisia gnaphalodes* more than 500, but Andropogon was intermediate with 300. A low linear production of rhizomes in a given area did not correspondingly limit the ability of a species to increase

its area. The increase of *Polygonum muhlenbergii* in loam was nearly three times that of *Artemisia gnaphalodes.* The new rhizomes produced by Polygonum were long but relatively few in number. Both production of rhizomes and increase in area by *Calamovilfa longifolia* were low. The individual rhizomes were comparatively short. This indicates that rate of increase depends upon the length of new rhizomes. If food expenditure is for aggregation of rhizomes rather than elongation, then a smaller area is more completely occupied.

Among species grown in duplicate in the two gardens, certain ones responded better to conditions in

sand, others to conditions in the low ground, while some responded about equally well to both. Percentage survival, general vigor of the plant, and gains in area were used as the standards for measuring response. *Andropogon scoparius, Panicum virgatum,* and *Sorghastrum nutans* developed better in sand. *Andropogon furcatus, Bouteloua curtipendula,* and *Bouteloua gracilis* appeared well adjusted to both habitats. All remaining species were more vigorous in the lowland garden. Since these experimental plants were not retarded by the severe competition found under normal conditions, a longer duration of the experiment would probably have resulted in the shifting of some species from one group to another.

The rhizomes of several species showed a tendency to seek lower levels in the experimental gardens than in natural grasslands. The maximum depth of the following species was from 2 to 4 inches greater under experimental conditions: *Artemisia gnaphalodes, Aster multiflorus, Aster salicifolius, Phalaris arundinacea, Solidago glaberrima,* and *Steironema ciliatum. Calamovilfa longifolia* was deeper in loam but not in sand. The loosening of the soil by plowing just prior to transplanting, thus providing better aeration, may have stimulated this response. Rhizomes produced by plants growing in natural habitats were often much shorter than those produced in the gardens (Table 5). This was probably a response to competition.

TABLE 5. Length in inches of rhizomes of the current year's growth in natural habitats.

Species	Maximum	Average
Agropyron smithii.............	38.0	10.0
Andropogon furcatus..........	2.0	1.0
Andropogon scoparius.........	1.0	0.5
Bouteloua curtipendula........	3.0	2.0
Bouteloua gracilis.............	0.75	0.5
Buchloe dactyloides...........	0.75	0.37
Calamovilfa longifolia.........	12.0	5.5
Elymus canadensis............	1.0	0.75
Panicum virgatum............	5.0	2.0
Phalaris arundinacea..........	4.0	2.5
Poa pratensis.................	12.0	——
Sorghastrum nutans...........	4.0	1.5
Spartina pectinata.............	12.0	6.0
Artemisia gnaphalodes........	12.0	7.0
Aster multiflorus..............	10.0	4.0
Aster salicifolius..............	18.0	——
Glycyrrhiza lepidota...........	67.0	50.0
Solidago altissima............	14.0	10.0
Solidago glaberrima...........	12.0	——
Steironema ciliatum...........	14.0	10.0

Several studies dealing with underground plant materials have been based on samples taken from the upper four inches of soil (Weaver and Harmon, 1935; Kramer and Weaver, 1936; Shively and Weaver, 1939). Of the species included in this study, only the following showed a normal depth range of rhizomes below four inches: *Calamovilfa longifolia, Glycyrrhiza lepidota, Polygonum muhlenbergii, Spartina pectinata,* and *Urtica gracilis.* Rhizomes of

Agropyron smithii and *Elymus canadensis* sometimes attain a depth of five inches. Most of the species included in this group are robust as well as deep.

Based on an average diameter of 3.5 mm. and the production of 319 ft. per sq. m., the computed volume of the rhizomes of big bluestem grown in the loam garden was 932 cc. per sq. m. Shively and Weaver (1939) found that one-half square meter samples of big bluestem taken from stations located in native grassland with an average annual precipitation of 26.3 inches produced an average volume of underground materials, including roots, of 1,187 cc. This volume was determined directly by displacement of water. When these data, obtained under somewhat different conditions and by different methods, are compared, more than one-third of the underground parts of big bluestem found in the surface four inches of soil consists of rhizomes. The ratios for little bluestem and western wheat grass thus attained are considerably smaller.

SUMMARY

1. An experimental study of the rhizomes of 24 species of prairie plants was made to secure exact information on habits of growth, on rates of spread in natural habitats and in two types of tilled fields, and on responses of certain species to desiccation and to deposition of soil.

2. Greatest gains in area were made by species equipped with propagating roots or with stolons, and the smallest by species largely dependent upon tillering. Advances by rhizomes were variable.

3. Rate of propagation by rhizomes was influenced by the time of initiation and the duration of the period of elongation, by the amount of elongation, by branching habits, by number of buds developed annually, and by growth of tops. There was no correlation between diameter of rhizome and rate of propagation.

4. The total length of rhizomes produced within a given area varied inversely with the diameter. When grown in tilled fields the rhizome production in feet per given area of certain forbs (*Artemisia gnaphalodes, Aster multiflorus, Aster salicifolius,* and *Solidago glaberrima*) compared favorably with that of the grasses with which they are normally associated.

5. Deeply placed rhizomes were usually robust, but shallow ones were not necessarily slender. Rhizomes growing naturally near the surface were either slender or robust.

6. Six species of grasses formed rhizomes or stolons within 60 days after emergence. Neither *Andropogon furcatus* nor *Sorghastrum nutans* possessed rhizomes after 100 days, but *A. furcatus* tillered early and freely. The first rhizomes of a seedling *Solidago glaberrima* originated from the root.

7. Rhizomes of *Agropyron smithii* and *Polygonum muhlenbergii* showed considerable ability to maintain viability through long periods of desiccation. The degree of resistance to desiccation in *P. muhlenbergii* varied with the stage of development of the plants, being greater before initiation of growth in spring.

8. *Andropogon furcatus* and *Bouteloua gracilis* recovered through not more than 3 inches of soil deposit. *Artemisia gnaphalodes, Aster multiflorus, Calamovilfa longifolia, Solidago glaberrima,* and *Spartina pectinata* all grew through as much as 6 inches, and *Agropyron smithii* penetrated through 12 inches.

9. Stolons of *Buchloe dactyloides* under optimum conditions elongated as much as 2.25 inches per day. Forage production from a thick stand of this grass exceeded that from native bluestem meadows.

10. *Andropogon scoparius, Panicum virgatum,* and *Sorghastrum nutans* responded more favorably to sandy soil. *Andropogon furcatus, Bouteloua curtipendula,* and *Bouteloua gracilis* responded equally well to both sand and loam. The other species, including the forbs, *Agropyron smithii, Buchloe dactyloides, Spartina pectinata,* and other grasses, were more vigorous in loam. These responses were probably reactions to differences in soil moisture and aeration in the two habitats.

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STRATIFICATION, DIURNAL AND SEASONAL MIGRATION OF THE ANIMALS IN A DECIDUOUS FOREST

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STRATIFICATION, DIURNAL AND SEASONAL MIGRATION
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INTRODUCTION

The movements of invertebrate land animals in response to temperature and humidity changes in the environment have engaged the attention of animal ecologists during recent years. Some animals are commonly found on the ground, others on the herbs, and still other species at different levels in the shrubs and trees. This is termed stratification. There have been a number of studies of the invertebrate life of forests in which the workers studied the animals by strata. Weese (1924) studied stratal and seasonal societies of an elm-maple forest. He took random samples from the ground, herb, and shrub strata for one year. Extensive meteorological observations were made during the period of study for the purpose of correlating the stratal and seasonal fluctuations in the animal population with changes in environmental conditions. He found seasonal variations in the animal populations to be, in general, in inverse ratio to variations in the evaporating power of the air and observed a marked increase in the insect population in the early autumn probably due to an influx of species, preparing for hibernation, from meadows and forest borders. The inward migration occurred at the same level the insects normally occupied during the summer and was followed by a downward migration to the place of hibernation. There was a similar increase followed by an upward and outward migration in the spring. Davidson (1930), in a study of the tree layer society of the maple-red oak climax forest, found some species to be characteristic for certain heights in trees. Among these species were the following spiders: *Eustala anastera* Walck., *Bathyphantes alboventris* Banks, *Araneus labyrinthus* Htz., *Araneus curcubitinus* Clerek., *Marpissa* sp., *Theridion murarium* Em., and *Theridion punctosparsum* Em. These spiders were found only in the trees. Among six species of beetles that she found in the tree layer society during the estival and serotinal societies were: *Cantharis excavatus* Lec. and *Ptilodactyla serricollis* (Say). *Cantharis excavatus* was collected from the herb and shrub strata during the estival society and from the trees in the serotinal society. *Ptilodactyla serricollis* was taken only from the tree sweepings at seven meters though Blake (1926) reported it in the leaf stratum during the winter. Most of the species were found at only one or two levels in the trees but a few species, as *Dictyna* sp. and *Xysticus* sp. among the spiders, were taken in the herb and shrub strata and at most of the levels at which collecting was done in the trees. These studies seem to indicate the presence of definite stratal societies with stratal changes being due to seasonal influences.

Although these studies were concerned with stratal societies, there have been scattered references in the literature that seemed to indicate diurnal movements from one stratum to another. Do animals remain in definite strata or do they move from one stratum to another in response to environmental changes? If some of the animals move from the ground and herbs to the herbs and shrubs or from the herbs and shrubs to the trees during the morning and make reverse movements in the late afternoon, they should offer valuable aid to the ecologist since they are free to move in response to changed conditions. According to Sanders and Shelford (1922), "Animals free to shift back and forth are a much more sensitive index than plants." They studied the animal population of a pine-dune community during a period of two months by taking collections from the different strata and making a quantitative report of the animals found. To check a suspected diurnal movement, collections were made at four-hour intervals for a period of two days (July 15 and August 14). They observed a horizontal migration of water-breeding species from a nearby swamp and found some evidence of diurnal vertical migration but the study seems too brief to justify generalizations. The diurnal migration of insects from one plant association to another was studied by Gudoshchikova (1927). During the summer, he found variations in the numbers of animals caught in the same layer of the same community at different times of the day. He made a careful study, for one day, of the populations of the plant associations from which he had been collecting, to verify apparent diurnal migrations. The communities from which he collected these data were located: on the sand of a river bed, at the foot of a flood plain terrace; on a sand ridge above; and on the margin of the terrace. It seems that the meteorological factors of these communities showed some similarities to those of the strata in a forest. He found the total population, the Nematocera, and the Cicadellidae to show a positive reaction to temperature, by moving into the community in which the temperature was higher at the particular time, with the reaction to relative humidity negative or absent while the Brachycera followed temperature differences only when the relative humidity was higher than 87 per cent. However, his study of diurnal migrations was for a single day and the animal variations of other days might not show the same results.

The stratal conception of animal distribution presumes that certain species are peculiar to a stratum or are found there in much greater numbers than in other strata. This would mean that there is little diurnal vertical movement. If it were found that there was a considerable diurnal movement of the animal population from stratum to stratum, then the concept of strata in ecology would lose much of its significance.

Since the problem of the migrations of terrestrial invertebrates is one that has been considered as having special significance in animal ecology and since previous work has been inconclusive with respect to the diurnal movements of these animals, the writer attempted an extended quantitative study in a deciduous forest. The study covered a longer period of investigation of diurnal vertical movements than any of the studies previously mentioned and should indicate diurnal vertical migrations of the insects of a deciduous forest in response to meteorological changes if there are such movements of any consequence. If the study shows no definite evidence of a regular diurnal migration, the results should be significant in substantiating the studies that have indicated a definite stratification of species. These are the reasons for the present study.

The work was carried out under the supervision of Dr. Jesse M. Shaver of George Peabody College for Teachers, Nashville, Tennessee and the writer wishes to express to him sincere thanks for his interest and helpful suggestions. The writer is also indebted to Dr. T. A. Frick for naming the plants in the area studied. Acknowledgments for taxonomic work are due the following: Nathan Banks and Elizabeth Bryant, mites and spiders; H. A. Pilsbry, Mollusca; R. V. Chamberlin, Chilopoda and Diplopoda; D. M. DeLong, Cicadellidae; and the following members of the Bureau of Entomology, United States Department of Agriculture, and their collaborators: C. F. W. Muesebeck, Braconidae, Serphoidea, and Bethylidae; A. B. Gahan, Chalcidoidea; G. A. Sandhouse, wasps; R. A. Cushman, Ichneumonidae; L. H. Weld, Cynipidae and Figitidae; W. M. Mann and M. R. Smith, Formicidae; C. T. Greene, David G. Hall, Alan Stone, and J. M. Aldrich, Diptera; E. A. Chapin, H. S. Barber, W. S. Fisher, and L. L. Buchanan, Coleoptera; H. G. Barber, Hemiptera; P. W. Oman, Homoptera; P. W. Mason, Aphididae; A. N. Caudell and A. B. Gurney, Neuroptera, Orthoptera, and Corrodentia; August Busck, J. F. Gates Clarke, and Carl Heinrich, Lepidoptera; J. W. Folsom, H. B. Mills, and H. E. Ewing, Thysanura and Collembola.

AREA STUDIED

LOCATION

The young elm-maple stage of a deciduous forest climax in which this study was made was in Percy Warner Park, a natural forest, thirteen miles southwest of Nashville, Tennessee (Fig. 1). The circle shows the exact location of the station. This park, at that time, contained 2,500 acres of deeply wooded forests and rolling blue grass fields. The high hills contained a great variety of native deciduous trees, shrubs, and wild flowers. The 700 foot contour line ran through the part of the park in which the study was made.

GEOLOGY

According to Mistler (1937), who studied the geology of the Radnor Lake area not far from Percy Warner Park, the rocks exposed in the area mapped
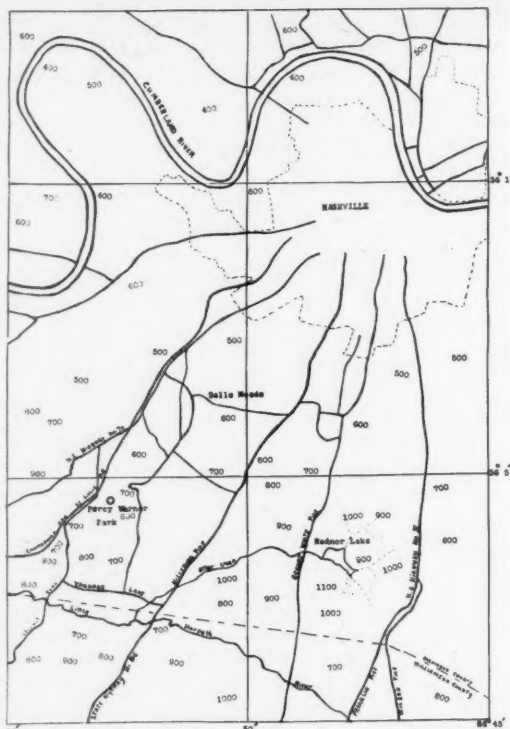
Fig. 1. Map showing location of Percy Warner Park. (From U. S. Geol. Survey Map of the Nashville Quadrangle.)

range in age from the Cannon limestone of the Ordivician Period to the Osage group of the Mississippian Period. The Leipers Formation of the Ordivician Period outcrops a considerable distance up the slopes and the hills are topped with Ft. Payne chert resting upon Chattanooga black shale. The rocks underlying the habitat studied, therefore, are blue and grey limestone very probably of the Leipers Formation.

CLIMATE AND WEATHER

The following summary of meteorological conditions during the period of this study was taken from a compilation made at the Weather Bureau Station at Nashville, Tennessee, by Jones (1932) and Williamson (1935 and 1938) for the years 1931, 1932, and 1937.

The fall of 1931 was characterized by a high precipitation in December, although the average for the year was below normal. The temperature was higher than normal, with a mean annual temperature of 61.6° F. The relative humidity was about normal for November but above the normal in December. The first killing frost of the autumn was on November 7. This was ten days later than the average date.

The year 1932 had a precipitation of 50.53 inches which was higher than the average for a long period

of years. The greatest monthly precipitation was in January of that year, with a precipitation of 7.74 inches, and the lowest was in May with a precipitation of 1.32 inches. The precipitation was greater than the normal during January, February, and April, and less than normal for March, May, June, July, and August. The mean annual temperature was 60.5° F. The mean temperature was higher for January and February, 1932, than the normal for those months, while the mean temperature for February was higher than the means of January and March with March having a mean 5° F. below the normal. The remaining months until August showed increasing mean temperatures with 15° F. increase from March to April, 8.5° F. increase from April to May, and 10.5° F. increase from May to June. June, July, and August varied little with respect to mean temperature, although they were slightly above the normal. Relative humidity was higher than normal in January; about normal in February, March, and April, and less than normal in May, June, July, and August although only slightly less in June and July. The latest killing frost, in the spring, was on March 23. This was eight days earlier than the average date. December, 1931, had only 82 hours of sunshine as compared with 170 hours for November of that year and 144 hours for December, 1937. For the months, January through August, 1932, the sunshine hours were about normal with February and July being above normal and April and June below normal.

During the fall of 1937 the precipitation was greater than the normal for October and rains interfered with the collections on a number of days. The precipitation was less than normal during November and December and less than that for the corresponding months of 1931. The mean temperature during October, November, and December was lower than normal and lower than the temperature during the same months of 1931 although the mean annual temperature was 59.3° F., which approximated the average of a long period of years. Relative humidity was above normal during these three months and increased from October to December. The first killing frost was on October 24. This was four days earlier than the average date and two weeks earlier than in the fall of 1931 when the collections were begun. There were more cloudy days in October and December than in November. November was about normal in this respect.

VEGETATION

The trees were predominantly young sugar maples (*Saccharodendron barbatum* (Michx.) Nieuwl.), and white elms (*Ulmus americana* L.). White hickory (*Hickoria alba* (L.) Britton), red mulberry (*Morus rubra* L.), sassafras (*Sassafras Sassafras* (L.) Karst.), and a few yellow oaks (*Quercus Muhlenbergii* Engelm.) were scattered throughout the habitat with a large sycamore (*Platanus occidentalis* L.) at the southwest limit of the station. A number of tulip trees (*Liriodendron Tulipifera* L.) were just outside of the station limit. Tulip, white hickory, black wal-

nut, and a few large beeches were the principal trees above the station.

The characteristic shrubs of the habitat were: spice bush (*Benzoin aestivale* (L.) Nees.), coral berry (*Symphoricarpos Symphoricarpos* (L.) MacM.), and pawpaw (*Asimina triloba* (L.) Dunal.). Poison ivy (*Toxicodendron radicans* (L.) Kuntze) and Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.) were attached to many of the trees with the poison ivy very common on the forest floor. A number of elms and maples were shrub size when the 1931-32 collections were made. Figure 2 is a chart of the woody plants of the station.

The spring herbs have not been studied for that particular station but herbs known to be present in that part of the park are: spring beauty (*Claytonia virginica* L.), rue anemone (*Syndesmon thalictroides* (L.) Hoffmg.), toothwort (*Dentaria laciniata* Muhl.), blood root (*Sanguinaria canadensis* L.), violet (*Viola Papilionacea* Pursh.), and phlox (*Phlox divaricata* L.). The herbs of the fall season were: bedstraw (*Galium pilosum* Ait.), white snakeroot (*Eupatorium urticaefolium* Reichard), white bane berry (*Actaea alba* (L.) Mill.), jump-seed (*Tovara virginiana* (L.) Adans), and *Polygonum* sp. Some coral berry bushes were at herb height in 1931 and 1932. Of the ferns, *Asplenium platyneuron* (L.) Oakes and *Botrychium virginianum* (L.) Sw. were the most common.
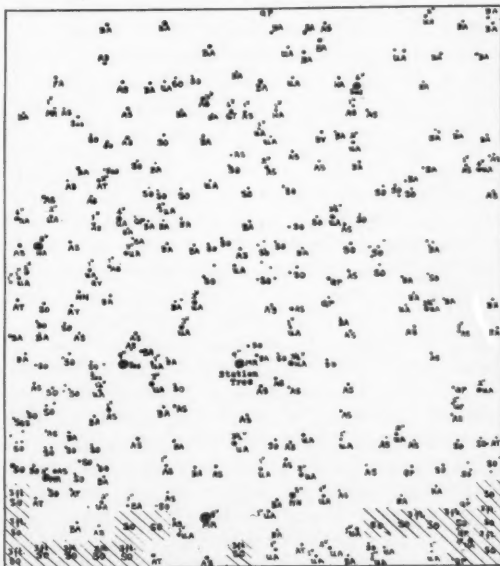
FIG. 2. A chart of the woody plants of the station. The area charted was 54 by 60 feet. The figures represent inches in diameter at breast height. Shaded areas contained many *Symphoricarpos Symphoricarpos*. Abbreviations: AS, *Saccharodendron barbatum*; AT, *Asimina triloba*; BA, *Benzoin aestivale*; DV, *Diospyros virginiana*; FA, *Fraxinus americana*; GT, *Gleditsia triacanthos*; HA, *Hicoria alba*; MR, *Morus rubra*; NN, *Negundo Negundo*; QP, *Quercus Muhlenbergii*; QV, *Quercus velutina*; Sas, *Sassafras Sassafras*; SO, *Symphoricarpos Symphoricarpos*; UA, *Ulmus americana*.

METHODS

COLLECTIONS

Since a part of the study was an attempt to determine whether there was a diurnal movement of the invertebrate animals in the forest, random samples of the animal population were taken in the early morning, at noon, and in the late afternoon from the leaf, herb, shrub, and tree strata. The leaf mat collections (called in the graphs: animals of the ground, and animals of the leaves) were taken from different parts of the station with an attempt made only to select comparable areas from the standpoint of thickness of the leaf mat, for these collections for any one day. The sampling of the herbs and shrubs was done by walking through the station and making sweeps back and forth in the vegetation. The tree sweepings were taken from a large red mulberry tree, containing grapevines, and from young maples and elms that could be reached from the limbs of this tree. The collections from the herb, shrub, and tree strata were made as nearly as possible, at the following heights: herbs, 1.5 feet; shrubs, 3 feet; and trees, 15 to 25 feet. These collections were made each Saturday from November 21, 1931, to August 20, 1932. Collections were also made twice weekly from October 2 to November 20, 1937, and once each week from November 20 until December 25, 1937.

The leaf mat collections were made from one square foot of leaf mold by placing a box-shaped tin, attached to a one-foot square wooden frame base, down on the leaf mold and carefully going over the leaves at once. The animals were placed in a vial containing 70 per cent alcohol. When the insects were very active the inside walls of the tin apparatus were coated with a syrup to prevent the escape of Diptera and leafhoppers that might fly up against the sides. Careful handling enabled one to catch the animals of the unit leaf area with only the occasional loss of a specimen.

The herb, shrub, and tree strata were sampled by taking ten short sweeps in each stratum with an insect net with a circular opening that averaged 30 cm. This is essentially the method of netting used by Weese (1924). The net, containing the collection, was placed in a large bucket and the animals were etherized. The specimens were then placed in a vial of alcohol properly labeled for time and stratum.

The collections were reported on the basis of one square meter. The leaf collections were multiplied by eleven and the herb, shrub, and tree collections by the factor four to bring them to this unit. These factors were arrived at after checking the collections, made in the usual way, with those made by enclosing a measured area with a large, cylindrical bucket that was pressed firmly into the soil and ether poured into an opening in the bottom. The bucket was removed after the animals were etherized and the vegetation and ground were gone over carefully for the animals. According to the estimate, forty sweeps of the net, of approximately one meter each, represented the animal population of one square meter. This method

was used by Smith (1928), Shackleford (1929), and others. Smith and Shackleford used fifty short sweeps of the net to represent the animal population of one square meter. According to Beall (1935), the size of the fraction, sweep catch to cylinder catch, must vary for different species at the same time and for the same species at different times. He found that between six and nine 100-inch strokes of the net indicated the population of one square meter. In speaking of the netting of leafhoppers, DeLong (1932) states that "a very rough inaccurate estimate is the best that can be hoped for by the sweep method for these active insects."

Various problems present themselves to the investigator of the relative animal populations of the different strata in a forest and the stratal changes of these populations. It is hard to make the collections comparable in the herb, shrub, and tree strata because of the increasing difficulty of making accurate sweep catches in the shrubs and trees. The limbs of the plants in the latter strata retard the sweeps and some of the insects may be lost as the force of the stroke is lessened. Thus, the netting is evidently more efficient in the herb stratum and decreases in efficiency in the shrub and tree strata in the order named. This factor was mentioned by Phillips (1931) and DeLong (1932). They also gave temperature as an important factor in the netting of insects, since it affects the metabolic rate and, therefore, the rapidity of the "jump" reaction. Davidson and Shackleford (1929) found periods of relative inactivity of the invertebrates of an Oklahoma prairie to result in larger collections. These were the periods between midnight and 3 a.m. and between noon and 3 p.m. Wind has been recognized as affecting the efficiency of netting. DeLong (1932) emphasized this particularly as a factor in the estimation of leafhopper populations. While Phillips and DeLong doubt the value of netting in obtaining an accurate estimate of relative populations, Beall (1935) states that "Sweep samples which give only a poor estimate of the population of an area may still be useful as indicators of various population phenomena. Thus seasonal fluctuations in the size of population have been determined without knowing the actual size of the population. Also aggregation might be demonstrated by the extent of variation from sweep to sweep even if the results gave no estimate of the total population present."

INSTRUMENTATION

The environmental factors studied were temperature, relative humidity, evaporation, and light. Maximum and minimum thermometers of the Six's type were used to measure the weekly maximum and minimum temperatures. These were calibrated against a standardized thermometer. They were placed as follows: beneath the leaves, on the leaf mold, 1.5 feet above the ground on a small maple tree by the station tree, 3 feet above the ground on the same maple tree, and 25 feet up in the station tree. These thermometers were read for weekly maximum and minimum temperatures and reset each Saturday at noon.

Beginning April 9, 1932, temperature readings were taken from these thermometers at the time collections were made in each stratum.

Relative humidity was measured by a hair hygrometer for the period from November 21, 1931, until August 20, 1932. From November 21, 1931, until February 13, 1932, the hair hygrometer was not calibrated daily. Consequently errors were probably made. For this reason, this data has not been used in the analyses in this paper. After February 13, 1932, the hair hygrometer was checked against standardized wet and dry bulb thermometers three times daily as used. Relative humidity was measured by standardized wet and dry bulb thermometers for the period from October 2, 1937, until December 25, 1937. The wet bulb thermometer was prepared by wrapping a rectangular piece of muslin one and one-third times around the bulb and tying firmly above the bulb. This was wetted in clean water immediately before using. The wet and dry bulb thermometers were held in the right hand and moved rapidly back and forth until a constant reading was obtained. The relative humidity values were determined by use of the Psychrometric Tables of Marvin (1915).

The evaporation rate, which may give the integrated effects of temperature, insolation, humidity, and wind, was measured by spherical porous cup atmometers during the late spring and summer of 1932 and in the fall of 1937 until freezing weather necessitated their removal. These atmometers were rainproofed by using mercury valves as developed by Livingston and Thone (1920). Both the black and white bulbs were standardized against black and white bulbs of known coefficients by mounting them upon an apparatus made from a bicycle wheel and rotated by directing an air current from an electric fan against heavy cardboard vanes to cause the wheel to make eight or less revolutions per minute. Readings were taken before and after the wheel had operated for twenty-four hours and correct coefficients were determined by comparison with the standards. This method was first described by Nichols (1913).

A black and white bulb atmometer were exposed in each stratum as follows: in the leaf stratum on the northwest side of the station tree with the bulbs on a level with the leaf mat; in the herb stratum on the northwest side of the station tree with the bulbs 1.5 feet above the ground; 3 feet above the ground on the northwest side of the station tree; and 25 feet up in the station tree. Those in the tree were protected by a guard of coarse wire netting.

The atmometer reservoirs were filled with distilled water from a graduated cylinder each Saturday and the results were recorded, after corrections were made, as the loss for the previous week. Formaldehyde was added to the water in the proportion of 200 cc. to five gallons of water to prevent the development of molds. Later, it was found necessary to add 375 cc. to five gallons of water.

Light readings were taken with a Macbeth Illuminometer in each stratum, from 4:50 a.m. until 6:40 p.m. on May 3, 1932, and from 5:00 a.m. until 4:50 p.m. on July 31, 1932. These days were taken as representative days with few clouds before full foliage development and after the leaves were well developed.

DIURNAL MOVEMENTS OF THE POPULATION

GRAPHICAL ANALYSES

The purpose of this section is to consider the animal populations of the different strata and the environmental factors of these strata from the standpoint of comparison of animal movements from one stratum to another with changes in physical factors. Two methods of treatment of these data were decided upon after a number had been tried and rejected. The first method used was a representation by graphs of the changes in the numbers of animals in each stratum from early morning until noon compared with temperature and relative humidity changes and another series of graphs to show similar comparisons from noon until evening. The method of preparation of these graphs needs detailed explanation. Figures 3 and 4 are used for this purpose. These graphs were prepared from the data collected from the time (April 9) of the considerable increase in the numbers of insects in the upper strata during the vernal society until August 20, 1932, and the data collected from October 2 until December 25, 1937.

The curve "animals on ground" will be explained first. The first point on this curve represents zero and not the total numbers of animals on the ground stratum. The second point represents the decrease in the collection made in that stratum at noon, April 9, as compared with the total numbers of animals found there in the morning. This difference is plotted to scale, each unit on the y-axis representing 100 animals. Therefore this curve shows that there was a decrease of 200 individual animals from the time of the morning collection to noon in the ground stratum on April 9. The point of the curve representing noon, April 9, is now considered zero and stands for the morning collection of April 16. The next point shows the increase of the noon collection over the collection of the early morning on April 16. Thus, only differences were plotted to scale. In a similar way, the total animals found in each of the other strata (animals in herbs, animals in shrubs, animals in trees) were plotted to show changes in the total population from morning to noon, using the same scale as for animals on ground. The temperature curve for the ground stratum was similarly prepared by plotting the difference in the temperature of the ground in the early morning and at noon. In this case, one unit of the y-axis represents 20° F. Relative humidity was plotted in the same way for the herb stratum with each unit of the y-axis representing 40 per cent relative humidity. Thus, two points were used to represent each group of data for each date and, rather than starting at a base line each time, the data for each successive date were plotted on the last point of the preceding date. This might be termed a graph of increments.
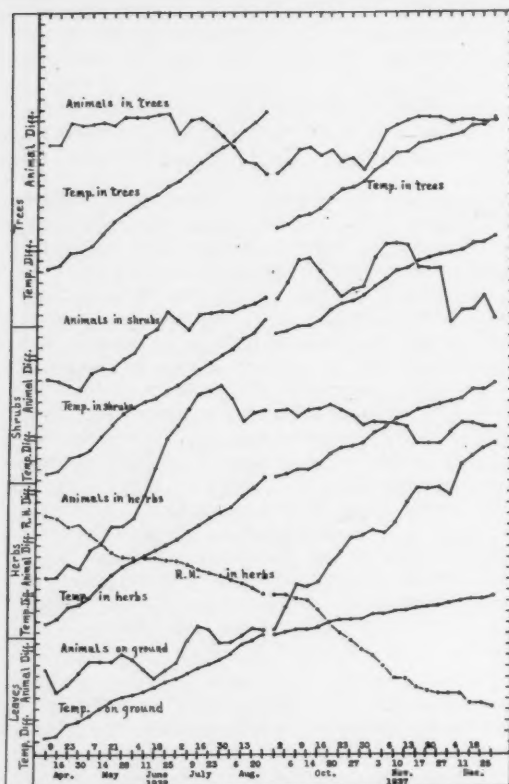
FIG. 3. Changes in total numbers of animals and certain physical factors from morning until noon.

Figure 4 was plotted in a similar way to Figure 3 except that the curves deal with changes from noon until night and each unit of the y-axis represents 16° F. for the temperature curves and 16 per cent for the relative humidity curve.

In addition to these graphs of total population changes, three groups of insects were selected for a similar analysis. Diptera; Hymenoptera, exclusive of ants; and Cicadellidae were considered as being more likely to show diurnal vertical movements. Species were not treated in this manner because there were few caught over a sufficiently long period of time and since many of the abundant Diptera and Cicadellidae could be determined, even by specialists, only to families or genera. Increment curves, similar to those just explained, were plotted, but using different scales, for these insect groups (Figs. 5-10).

Having now explained the construction of the curves, there remains the task of determining what each graph indicates. There was an increase in the noon collection of the total population on the ground (Fig. 3) over the early morning collections more often than not in the spring and summer and definitely more often in the autumn and early winter. The general upward tendency of the curves for morning to noon

differences of the total population of the ground, herb, and shrub strata during the spring and early summer, seems to indicate no diurnal movement between these strata since, as a rule, there are no increases in one stratum with corresponding decreases in another. They do show an increase in numbers of animals caught, for this period, in these strata as temperature increased and relative humidity decreased. On the other hand, the trend of the curve for the tree stratum during the spring and summer seems to indicate that at least some species move out of the tree stratum as temperature increases and relative humidity decreases. The reverse seemed to be the case for this stratum during the autumn and early winter when the stresses of temperature and evaporation were not so great. The upward trend of the curve for animals on the ground, during the autumn and early winter would be expected because of the presence of more hibernating species, and other insects such as ants, in the noon collections from this stratum as they came from more protected locations as the temperatures increased during the day.

The differences in total animals from noon until night (Fig. 4) show decreases in the late afternoon collections from the shrub and tree strata on most of the dates of collection from spring through the
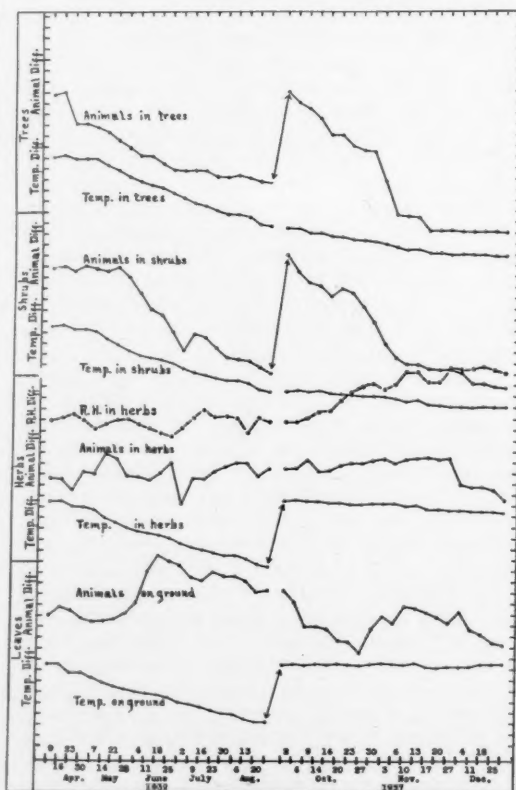
FIG. 4. Changes in total number of animals and certain physical factors from noon until night.
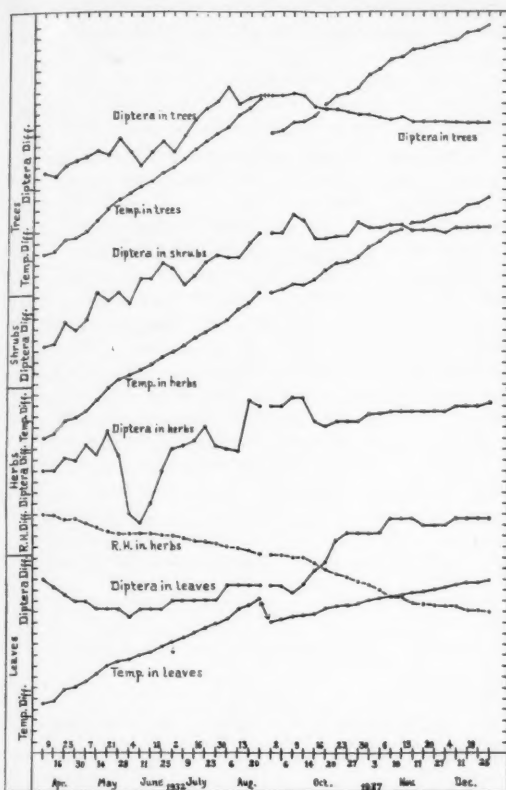
FIG. 5. Changes in numbers of individual Diptera and certain physical factors from morning until noon. Values of y-axis: 16 Diptera, 20° F. temperature, and 80 percent relative humidity. The term "in leaves" refers to leaves on ground.

autumn. There were no regular increases in the late afternoon collections of the herb and ground strata although the curve for the herb stratum had a slight upward trend. This upward trend of the curve of this stratum is not great enough to account for a downward migration to the extent indicated by the curves of the shrub and tree strata, however, and it seems that factors other than diurnal migration must be concerned. With the exception of the periods from May 7 until June 18 and from October 27 until November 10, there were decreases of the evening collections of the ground stratum. These decreases might be accounted for by a movement of some of the animals into the soil. These periods showing increases, however, were dates on which there were pronounced decreases in the shrub and tree strata. Thus, there was a decrease in numbers of animals in the evening catches of the shrub and tree strata, as temperature decreased, with only a slight gain in the herb stratum and an occasional gain on the ground. Relative humidity decreased from noon until late afternoon about as often as it increased during the spring and summer but increased rather regularly in

the late afternoon during the autumn and early winter. The curves for total animal differences did not seem to be related to the relative humidity curve to any appreciable extent.

There was, in general, an increase in the number of Diptera caught in the noon collections of the shrub and tree strata during the spring and summer with only an occasional decrease in the collections of the ground or herb strata (Fig. 5). These increases were accompanied by increases in temperature and, usually by decreases in relative humidity. There are some dates on which increases in the shrub and tree strata were accompanied by decreases in the herb stratum (May 7, 21, July 23, Aug. 20) but, in general, there was a rather consistent increase in numbers of Diptera in all three of these strata although less regularly so in the herb stratum.

There was, with some variations, a decrease in the numbers of Diptera, noon until night, in the trees and shrubs for the spring and summer seasons with temperature decreases and no apparent relation between Diptera changes and relative humidity changes (Fig. 6). The numbers of Diptera increased in the late
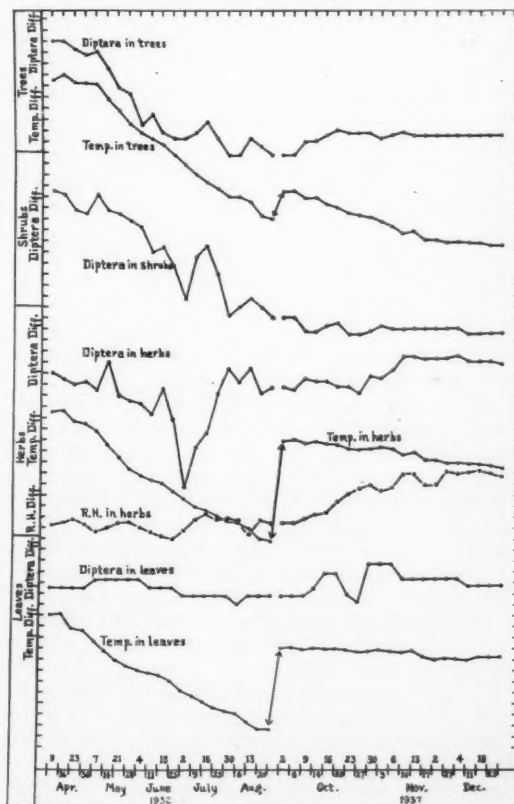
FIG. 6. Changes in numbers of individual Diptera and certain physical factors from noon until night. Values of y-axis: 16 Diptera, 8° F. temperature, and 16 per cent relative humidity. The term "in leaves" refers to leaves on ground.
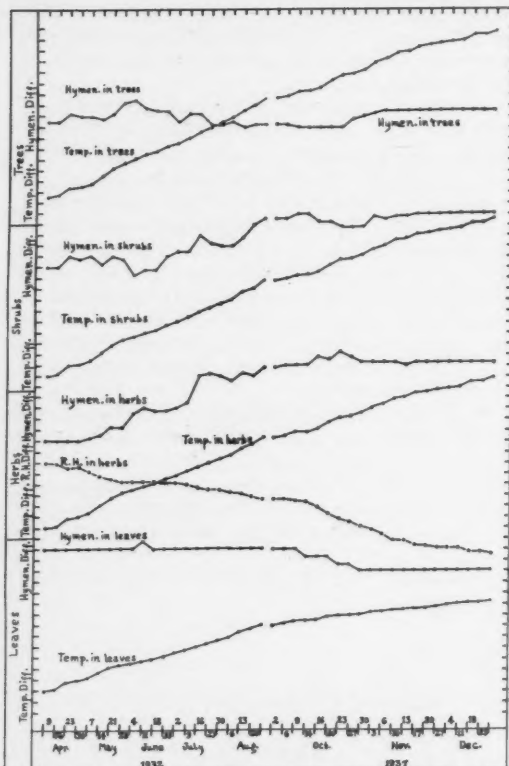
FIG. 7. Changes in numbers of individual Hymenoptera and certain physical factors from morning until noon. Values of y-axis: 16 Hymenoptera, 32° F. temperature, and 80 per cent relative humidity. The term ''in leaves'' refers to leaves on ground stratum.

erease and decreased more regularly with temperature decrease than in the herb stratum, there were often increases or decreases in all of the strata at the same time. This seems to indicate the possibility of lateral migration of these insects or that physical factors affected the catches at different times of the day.

The morning to noon differences in the number of Hymenoptera as compared with temperature and relative humidity changes show (Fig. 7) that Hymenoptera increased more markedly in the herbs from morning until noon than in the shrub stratum and more regularly in the shrubs than in the trees. In fact, the Hymenoptera increments in the noon tree collections indicate decreases in numbers about as often as increases. Again, as in the case of Diptera, the morning to noon increase is greater for the spring and summer seasons than in the autumn and in early winter. On the other hand, the Diptera increases at noon were more consistent in the upper strata than in the herb stratum. This may mean a greater tendency for the Hymenoptera to increase more in the lower strata with increase in temperature and decrease in relative humidity. This would mean that there is a downward movement from morning until noon if

afternoon collections about as often as they decreased. There were three dates (May 7, July 23, August 20) on which there was evidence of a diurnal migration upward from morning until noon and a movement in the opposite direction from noon until late afternoon. On these dates particularly there were decreases in the late afternoon catches of Diptera in the shrubs and trees with accompanying increases in the late afternoon collections of these insects in the herb stratum. No significance could be attached to the variations of Diptera in the leaves since there were few changes in the numbers caught there. None of the curves show sufficient changes for consideration during the autumn and early winter.

For the Diptera variations from morning until noon (Fig. 5) and from noon until night (Fig. 6) to show definite diurnal vertical movements, the upper strata should show increases of these insects while the lower strata should show decreases or vice versa. For example, it seems that increases of Diptera in the shrubs and trees should be accompanied by corresponding decreases in the herbs if there is a diurnal movement. While the number of Diptera in the shrubs and trees increased more definitely with the temperature in-

FIG. 8. Changes in numbers of individual Hymenoptera and certain physical factors from noon until night. Values of y-axis: 16 Hymenoptera, 16° F. temperature, and 16 per cent relative humidity. The term ''in leaves'' refers to leaves on ground stratum.
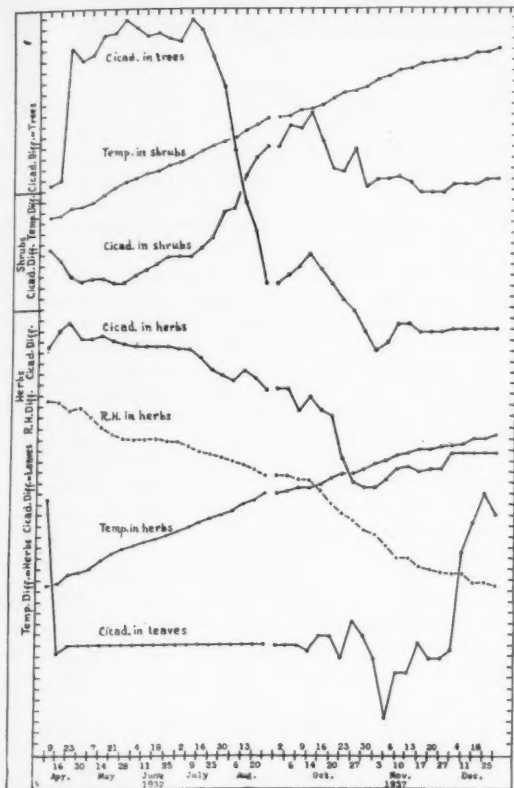
FIG. 9. Changes in numbers of individual Cicadellidae and certain physical factors from morning until noon. Values of y-axis: 16 Cicadellidae, 32° F. temperature and 40 percent relative humidity. The term ''in leaves'' refers to leaves on ground stratum.

there were accompanying decreases in the tree stratum. This seems to be true only on a few dates.

The changes in numbers of Hymenoptera from noon until night (Fig. 8) seemed to show, in general, some decrease in the numbers of these insects although the changes were not very marked, the decreases not being so definite as those of Diptera. There seemed some tendency for the Hymenoptera to decrease more in the herb and shrub strata with decrease in temperature and increase in relative humidity than in the tree stratum. This would seem to indicate some upward movement of these insects in the late afternoon if there were accompanying increases in the tree collections. This, however, was rarely the case.

After the seasonal migration that occurred during the first two weeks in April, there were some morning to noon increases of Cicadellidae (Fig. 9) in the trees until May 21 with no change or some decrease in the herb and shrub strata. From May 21 until August 20, however, there was a decrease in herb and tree strata with an increase in the shrub stratum. Since the temperature increased from morning until noon

during the spring and summer and, in general, relative humidity decreased, this would indicate a shrub-wise movement with increasing temperature and decreasing relative humidity. This increase of Cicadellidae in the shrubs from morning until noon was fairly definite until October 9. From that time, there were usually decreases at noon in all of the strata, possibly due to rains at the time of collections and the high winds at noon that characterized that period. During the winter, leafhoppers were usually more abundant in the leaf collections at noon. They probably came from beneath pebbles, small clods of dirt, and sticks under which they were in an inactive condition when the temperature was lower. At this season of the year, leafhoppers appeared in the upper strata, to some extent, on warm days although there was no vegetation on which to feed. Thus, it seems that diurnal vertical movements of leafhoppers from morning until noon, if shown at all, occur in the hot part of the summer when there is a movement into the shrubs and in the winter when they appear in the upper strata on warm days. It seemed that food plants determined, to a considerable extent, their distribution during the summer since many were observed in the
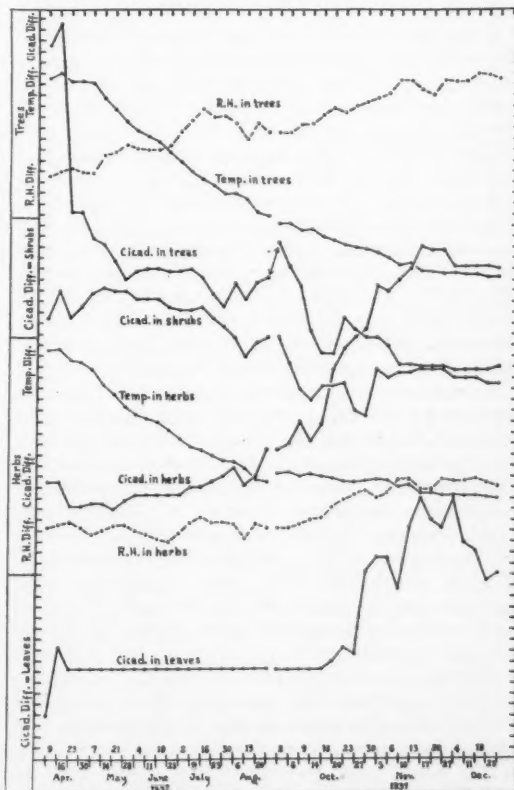
FIG. 10. Changes in numbers of individual Cicadellidae and certain physical factors from noon until night. Values of y-axis: 16 Cicadellidae, 8° F. temperature, and 16 percent relative humidity. The term ''in leaves'' refers to leaves on ground stratum.

trees in the early morning feeding upon foliage especially of grapevines.

The noon to night differences of Cicadellidae (Fig. 10) show a decrease in the late afternoon collections of the tree stratum, after the seasonal migration of early April, until May 28. For the same period there were some increases in either the herb or shrub stratum or both of these, with the exception of May 14. There was not much change in June but in July there were some decreases in the number of Cicadellidae in the shrub and tree strata with an increase in the herb stratum. The Cicadellidae differences from morning until noon showed, with few exceptions, decreases in the noon collections of the shrub and tree strata from October 2 until November 6 with some increases in the herb collections. The decreases in the late afternoon collections of the shrub and tree strata, for the period October 9 through October 30, might have been greater had it not been for the fact that the numbers of these insects had already decreased in the noon collections of this period. When there were increases in the afternoon collections of leafhoppers from the leaves without accompanying decreases in the upper strata one would suspect a possibility of one or more factors affecting this change. The leaf mat from which these collections were made necessarily varied in leafhopper population during the winter in different parts of the station due to the number and dryness of the leaves. This study of Cicadellidae seems to indicate a downward movement of these insects in late afternoon from the shrub and tree strata into the herb stratum during a part of the summer season and in the autumn. This means a downward movement as temperature decreased and as relative humidity increased. However, there were no consistent increases of relative humidity at the time of the late afternoon collections of the spring and summer. A daily study of these insects when seasonal migratory movements are not involved might reveal more definite diurnal movements.

In general, the curves of Figures 5-10 show an increase of the animal catches from morning until noon. These increases were more definite in the shrub and tree strata than in the herb stratum for Cicadellidae, and more regular in the herb and shrub strata for Hymenoptera and total animals. For the noon to night changes, the curves generally show decreases of the animals caught in the late afternoon collections. Diptera, Cicadellidae, and total animals decreased more definitely in the shrub and tree strata with some gains in the herb stratum while Hymenoptera decreased somewhat more regularly in the herb and shrub strata than in the tree stratum.

Thus, it appears that more animals are caught in midday collections than in the early morning and fewer in the late afternoon collections than at noon in the shrubs and trees with the reverse sometimes the case for herb and leaf collections but not regularly so. It is also apparent that there were different reactions on the part of different groups of animals to changes of physical factors.

From a comparison of the movements of the animals with temperature variations, it seems that there was an increase in the number of Diptera in the shrub and tree strata, a more pronounced increase of Cicadellidae in the shrub stratum than in the other strata, and a greater increase of Hymenoptera and total animals in the herb and shrub strata than in the tree stratum, with temperature increase. It is also apparent that there was a more definite tendency of Diptera, Cicadellidae, and total animals to decrease more regularly in the shrub and tree strata, and for Hymenoptera to decrease more regularly in the herb and shrub strata with temperature decrease. However, these changes of animals were apparently not proportional to the temperature changes.

A comparison of the changes in animal numbers with relative humidity variations seems to show more increase of Diptera in the shrub and tree strata than in the herb stratum, more increase of Cicadellidae in the shrub stratum than in the other strata, more increase of Hymenoptera and total animals in the herb and shrub strata than in the tree stratum, as relative humidity decreased. A consideration of the noon to night changes in animal numbers shows more definite decreases of Diptera, Cicadellidae, and total animals in the shrub and tree strata than in the herb stratum, and a greater decrease of Hymenoptera in the herb and shrub strata than in the tree stratum, as relative humidity tended to increase. Yet these changes do not appear to be proportional to the relative humidity variations.

CORRELATION STUDIES

Since many times with curves such as these there are things that escape careful observation, it is important to determine the coefficients of correlation by Pearson's product-moment or some other method of statistical treatment. In this case, since the writer was not concerned with changes in the total population as such, but only with the differences in the population from early morning until noon and from noon until late afternoon, it was thought that the method given by Yule (1922, pp. 197-201) would give better results than a treatment of total populations and temperatures, etc. Thus, the second method of treatment of the data of this section of the work was to correlate the variations of the animals from the early morning until noon with temperature variations for that time. The same treatment was given the animal changes and relative humidity changes. The noon to night variations in animal numbers, as well, were compared with temperature variations from noon until night and also with relative humidity variations for the same period. The total population and the three groups of insects treated by the first method; that is, Diptera, Hymenoptera, and Cicadellidae, were selected for this method of treatment. This method is one that seems especially useful in treating the type of data collected in this problem. When the relations between the values of two variables that have been observed for some period of time are considered, one may find that slower changes obscure more rapid ones that might show close agreement. In such cases, it may be important to correlate the differences and

not the values. The slower changes involved in these data are the seasonal changes of numbers of animals and of physical factors while the more rapid changes are the daily variations of animal numbers and of physical factors. In applying the method to the present problem, instead of considering the correlation between the number of animals in the early morning collection and the temperature at that time or the correlation between the number of animals in the noon collection and the temperature, only the differences in the animal catches of morning and noon and the differences of temperatures were used. As has already been stated, the same method was used for correlating noon to night differences of animal numbers with the temperature differences and for correlating animal differences of both morning to noon and noon to night with relative humidity differences.

The results of the application of this method in comparing animal variations with temperature variations, are shown in Table 1. The results of a similar comparison with relative humidity are shown in Table 2.

TABLE 1. The relation between variations in insect numbers and temperature variations.

Kind of Animals and Strata Correlated	Correlation Coefficients and Probable Errors	
	Morn to Noon	Noon to Night
Total Population:		
Trees..............	.100 ± .108	.490 ± .081
Shrubs.............	.088 ± .106	.481 ± .082
Herbs..............	.354 ± .093	.073 ± .106
Ground............	.347 ± .094	.072 ± .106
Diptera:		
Trees..............	.200 ± .102	.374 ± .092
Shrubs.............	.382 ± .091	.355 ± .093
Herbs..............	.134 ± .105	.073 ± .106
Hymenoptera:		
Trees..............	.103 ± .106	.534 ± .076
Shrubs.............	.307 ± .097	.308 ± .097
Herbs..............	.403 ± .089	.128 ± .105
Cicadellidae:		
Trees..............	.101 ± .106	.270 ± .099
Shrubs.............	.062 ± .106	.138 ± .105
Herbs..............	.222 ± .101	.131 ± .105

A consideration of the significance of the correlation coefficients obtained is important here. While no definite limits can be assigned for high or low correlation coefficients, the rules given by Cooke, (1936, p. 120) will be used. "When r is 0, there is no correlation; when r is less than .25, the correlation is negligible; when r is between .25 and .49, the correlation is low; when r is between .50 and .75, the correlation is fairly high; and when r is above .75, the correlation is high or significant."

The correlation coefficients for variations of the total population with temperature variations, from morning until noon, show only a low correlation for the ground and herb strata and show no evidence of correlation for the shrub and tree strata. For the

TABLE 2. The relation between variations in insect numbers and relative humidity variations.

Kind of Animals and Strata Correlated	Correlation Coefficients and Probable Errors	
	Morn to Noon	Noon to Night
Total Population:		
Trees..............	.099 ± .106	.216 ± .102
Shrubs.............	.007 ± .107	.618 ± .107
Herbs..............	.171 ± .104	.103 ± .106
Ground............	.318 ± .096	.206 ± .102
Diptera:		
Trees..............	.079 ± .106	.030 ± .107
Shrubs.............	.226 ± .101	.002 ± .107
Herbs..............	.078 ± .106	.140 ± .105
Hymenoptera:		
Trees..............	.229 ± .101	.168 ± .104
Shrubs.............	.159 ± .104	.280 ± .098
Herbs..............	.261 ± .099	.165 ± .104
Cicadellidae:		
Trees..............	.022 ± .107	.141 ± .105
Shrubs.............	.161 ± .104	.030 ± .107
Herbs..............	.280 ± .098	.160 ± .104

noon to night changes of the total population with temperature changes, the correlation coefficients approach a fairly high correlation for the shrub and tree strata but show no evidence of correlation for the herb and ground strata. These coefficients seem to indicate that the total population increased in the ground and herb strata during the warming-up portion of the day and decreased in the shrub and tree strata as the temperature dropped. That is to say, the animals seemed to increase in the lower strata with an increase of temperature and decrease in the upper strata with a decrease of temperature. This may mean that some insects were already in the shrubs and trees at the time of the early morning collections and that others, as ants, moved into the leaves and herbs from more protected situations on or in the ground. No causal relationship can be stated and this movement might have been caused, at least in part, by other factors such as an increase in light. The decrease in the numbers caught in the shrub and tree strata, with temperature decrease, may have been largely due to a decrease in the numbers of certain groups of insects in the late afternoon collections.

The coefficients for total population changes with variations of relative humidity are small although negative for all of the strata with the exception of the shrub stratum. An interpretation of the movements of the total animals in response to relative humidity variations seems impossible other than to say that there seems to be some negative reaction to variations of this factor.

Since it seemed that a study of the variations of particular groups of insects rather than total population variations might be more significant, the Diptera, Hymenoptera, and Cicadellidae are treated below.

The coefficients for morning to noon variations of Diptera, as compared with temperature variations,

while not large enough to be significant, are positive for each stratum. These coefficients are negligible for the tree stratum, low for the shrub stratum, and that of the herb stratum shows practically no correlation. These coefficients would evidently have been much higher for the spring and summer months, since the curves of Figure 5 show an inverse or no relation of these factors during the autumn and early winter, had they been calculated. The coefficients for noon to night differences of Diptera and temperature differences are low for the shrub and tree strata and show no correlation for the herb stratum. These low coefficients indicate increases in the number of Diptera caught in the shrub and tree strata with temperature increases in the morning and decreases in the number caught in these strata as temperature decreased. If the coefficients for the herbs had been fairly high negative coefficients, there would have been more reason to believe that there is a definite diurnal vertical movement of these insects but such is not the case. The correlation coefficients are about what one would expect from a study of Figures 5 and 6.

The coefficients for Diptera differences and relative humidity differences are negative, although too small to have any significance.

Hymenoptera increased more markedly with temperature increases in the herb and shrub strata, from morning until noon, than in the tree stratum (Fig. 7). The correlation coefficients for Hymenoptera changes and temperature changes indicate the same. The coefficient is negligible for the tree stratum and the coefficients are greater, but low, for the shrub and herb strata. Hymenoptera did not decrease greatly in the late afternoon collections of the upper strata and the coefficients for changes of these insects with temperature changes are low for the shrub and tree strata and negligible, but still positive, for the herb stratum. The coefficient for the tree stratum is higher than that of the shrub stratum but the very marked decrease of Hymenoptera from noon until night (Fig. 8) on October 6 may have unduly influenced this coefficient. These coefficients indicate increases in the numbers of Hymenoptera caught in the herb and shrub strata with temperature increases and decreases in numbers caught in the shrub and tree strata with temperature decreases.

The coefficients for Hymenoptera variations and relative humidity variations were negative and, although larger than those for Diptera, were too small to be significant.

The coefficients for Cicadellidae changes from morning until noon with temperature changes, while not significant, are negative for the tree and herb strata and positive for the shrub stratum. Since temperature generally increased from morning until noon, this may indicate a decrease of the Cicadellidae in the herb and tree strata with some increase in the shrub stratum. These coefficients are evidently due to the marked shrub-wise movements of these insects in the summer (Fig. 9). The coefficients for Cicadellidae

variations with temperature variations, noon to night, are too low to be significant although they are positive for the shrubs and trees and negative for the herbs. This may indicate a greater tendency for a late afternoon drop in the numbers of Cicadellidae in the shrubs and trees with temperature decreases and an increase in the numbers in the herbs at that time. If these coefficients were larger, this would indicate a diurnal vertical movement.

The coefficients for Cicadellidae variations and relative humidity variations, although not significant, do seem to indicate some decrease in the numbers in the herbs, morning to noon, and some increase in the herb collections of the late afternoon. Relative humidity tended to decrease from morning to noon and, therefore, a positive correlation of Cicadellidae numbers and relative humidity in the herb stratum would seem to mean a decrease of Cicadellidae in the herbs at that time. Conversely, for the noon to night changes, a positive correlation for the herb stratum would seem to mean an increase of Cicadellidae in the late afternoon herb catches.

It appears, from a study of this treatment of the data, that different groups of animals show differences of increases or decreases in numbers with variations of the same environmental factor. It seems that more Diptera were found in the upper strata with an increase of temperature while more Hymenoptera and total population were found in the lower strata with temperature increases. There was an indication of a possible shrub-wise movement of the Cicadellidae (Fig. 9). All groups seemed to show decreases in the upper strata as temperature decreased. These statements are all based on low correlation coefficients, however, and probably are not significant.

It seems that, in general, the animals increased as relative humidity decreased or vice versa, although the coefficients are all low with some so low as to be negligible. In fact, no correlation at all is indicated for differences of Diptera with differences of relative humidity.

These increases of animals with temperature increases and decreases with temperature decreases in all strata and, in general, increases of animals with relative humidity decreases, or vice versa, in all strata seem to indicate little, if any, diurnal vertical movements since a positive correlation for the upper strata and a negative correlation for the lower strata would seem to be necessary to indicate any marked diurnal vertical movement.

These methods of treatment of the data (graphical analyses and correlation studies) seem to show no definite diurnal vertical movements since the curves of the figures (Figs. 3-10) tend to show upward or downward trends for all of the strata and the correlation coefficients (Tables 1-2) are, as a rule, positive for all strata or negative for all strata. This appears to mean that there were usually morning to noon increases in the animal catches and, in general, noon to night decreases. There were certain days on which Diptera showed definite diurnal vertical movements and at certain times of the year (late summer and

early autumn), Cicadellidae seemed to make definite diurnal vertical movements.

This seems to show that most animals are rather regularly distributed as to strata although at times there are diurnal vertical movements, particularly of some groups, as has been observed during short periods of study by other workers. The results, therefore, substantiates the work of those who found a definite stratification of species.

SEASONAL MOVEMENTS OF ANIMALS

STRATAL RELATIONS

Since it was thought that a consideration of stratal changes in the number of insects from a seasonal viewpoint might throw some light on diurnal movements, the data were treated by comparison of the mean stratal catches of each month.

This method of treatment of the data was an arrangement, in tabular form, of the monthly mean collections of Diptera; Hymenoptera, exclusive of ants; and Cicadellidae so stratal comparisons could be made of the insects caught in the early morning, at noon, and in the late afternoon. These tables were prepared by taking the monthly means of the number of animals collected in each stratum at the three times of the day at which collections were made. Since the collections of 1932 were made weekly, the number of collections averaged in obtaining these means was not always the same and, since collections were made more frequently during October of 1937, the means of this month were obtained from a greater number of collections. The comparisons were made between the monthly mean collections of the herb and shrub strata, the herb and tree strata, and, in the case of the Cicadellidae, the ground and herb, and the ground and tree strata, for the months April and October, since these insects were abundant in the ground collections during these months. The same stratal comparisons were made for the Cicadellidae from May to August, inclusive, as in the case of Diptera and Hymenoptera. The differences are given below the paired strata with a plus sign meaning a greater number of animals in the stratum named first. A minus sign signifies more animals in the last named stratum. Table 3 will be used to illustrate this method. A comparison of the mean collections of the herb and shrub strata for the month of April shows a difference of + 0.8 animals for the early morning collections. This means a greater catch in the shrub stratum. At noon, a difference of + 4.0 shows an increase of the difference between the herb and shrub strata and, while both show increases of the mean noon catches for the month, there was a greater increase in the shrub stratum. However, while there were decreases in both strata for the mean evening catches, the difference of + 4.8 shows less decrease for the shrub stratum. The herb and tree strata were compared in the same manner and similar comparisons were made for the other months.

It appears from this method of stratal comparison, that Diptera (Table 3) increased rather consistently

TABLE 3. The stratal differences in abundance of Diptera for different hours (monthly means).

Month	Name of Strata	Average Number of Animals		
		Morning	Noon	Late Afternoon
April, 1932	Shrubs Herbs	9.6 8.8	20.8 16.8	18.4 13.6
	Dev.	+ 0.8	+ 4.0	+ 4.8
	Trees Herbs	4.0 8.8	9.6 16.8	6.4 13.6
	Dev.	− 4.8	− 7.2	− 7.2
May, 1932	Shrubs Herbs	43.0 108.0	49.0 82.0	37.0 77.0
	Dev.	−65.0	−33.0	−40.0
	Trees Herbs	40.0 108.0	42.0 82.0	16.0 77.0
	Dev.	−68.0	−40.0	−61.0
June, 1932	Shrubs Herbs	35.0 68.0	48.0 91.0	22.0 58.0
	Dev.	−33.0	−43.0	−36.0
	Trees Herbs	26.0 68.0	26.0 91.0	21.0 58.0
	Dev.	−42.0	−65.0	−37.0
July, 1932	Shrubs Herbs	35.2 43.2	38.4 43.2	36.0 76.6
	Dev.	− 8.0	− 4.8	−41.6
	Trees Herbs	16.8 43.2	36.0 43.2	31.2 77.6
	Dev.	−26.4	− 7.2	−46.4
August, 1932	Shrubs Herbs	4.0 22.7	16.0 44.0	10.7 34.7
	Dev.	−18.7	−28.0	−24.0
	Trees Herbs	17.3 22.7	13.3 44.0	13.3 34.7
	Dev.	− 5.4	−30.7	−21.4
October, 1937	Shrubs Herbs	9.3 15.5	10.2 14.2	8.9 15.6
	Dev.	− 6.2	− 4.0	− 6.7
	Trees Herbs	6.7 15.5	3.6 14.2	6.2 15.6
	Dev.	− 8.8	−10.6	− 9.4

in the noon collections of the herb, shrub, and tree strata and usually decreased in the late afternoon collections from these strata during the months of April, May, and June. This was true for the months July and August, with the exception of a considerable increase of the number of these insects in the herb stratum in the late afternoon during July and a decrease at noon in the tree stratum during August. There was little stratal change in the early autumn. This offers no evidence of a definite diurnal vertical migration of these insects although the sum of the means for these strata at the times of the collections seems to indicate some movement, possibly a lateral migration. The stratal changes of Diptera differed little, from month to month, with the exception of the late afternoon gain in the herb stratum during July, and show no marked effect of seasonal influence.

There were rather consistent increases of the noon collections of Hymenoptera (Table 4) from the herb

TABLE 4. The stratal differences in abundance of Hymenoptera for different hours (monthly means).

Month	Name of Strata	Average Number of Animals		
		Morning	Noon	Late Afternoon
April, 1932	Shrubs	1.6	6.4	4.8
	Herbs	2.4	4.0	4.8
	Dev.	− 0.8	+ 2.4	0.0
	Trees	0.8	2.4	0.8
	Herbs	2.4	4.0	4.8
	Dev.	− 1.6	− 1.6	− 4.0
May, 1932	Shrubs	16.0	9.0	12.0
	Herbs	10.0	19.0	21.0
	Dev.	+ 6.0	−10.0	− 9.0
	Trees	9.0	15.0	2.0
	Herbs	10.0	19.0	21.0
	Dev.	− 1.0	− 4.0	−19.0
June, 1932	Shrubs	8.0	17.0	6.0
	Herbs	14.0	16.0	16.0
	Dev.	− 6.0	+ 1.0	−10.0
	Trees	16.0	8.0	5.0
	Herbs	14.0	16.0	16.0
	Dev.	+ 2.0	− 8.0	−11.0
July, 1932	Shrubs	9.0	8.8	8.8
	Herbs	11.2	19.5	16.0
	Dev.	− 2.2	−10.7	− 7.2
	Trees	8.0	8.0	7.2
	Herbs	11.2	19.5	16.0
	Dev.	− 3.2	−11.5	− 8.8
August, 1932	Shrubs	2.7	16.0	6.7
	Herbs	13.3	20.0	13.3
	Dev.	−10.6	− 4.0	− 6.6
	Trees	12.0	10.7	5.3
	Herbs	13.3	20.0	13.3
	Dev.	− 1.3	− 9.3	− 8.0
October, 1937	Shrubs	5.8	6.2	5.3
	Herbs	5.3	6.2	5.0
	Dev.	+ 0.5	0.0	+ 0.3
	Trees	1.3	3.1	2.2
	Herbs	5.3	6.2	5.0
	Dev.	− 4.0	− 3.1	− 2.8

and shrub strata and, in general, decreases in the collections from these strata in the late afternoon. The numbers of these insects in the collections from the tree stratum increased at noon and decreased in the late afternoon during April and May but decreased in both the noon and late afternoon collections of June to August inclusive. This seems to show no evidence of any regular diurnal vertical movements although the noon and late afternoon decreases in the tree stratum during the summer may have some significance. This suggests the possibility of the stress of physical factors causing a decrease of these insects in the tree stratum during this season.

Some evidence of diurnal vertical movements of Cicadellidae was shown (Table 5) for the months April to May since there were gains in the upper and losses in the lower strata at noon and the reverse in the late afternoon. A shrub-wise movement is shown by the noon collections of June, July, and August with a downward movement into the herbs

indicated by the afternoon collections. There was a decrease in the noon collections of all strata for the month of October with late afternoon increases in the herb and ground strata. The possible cause of this decrease at noon was suggested in the discussion of Figure 9.

There seemed to be little seasonal influence upon the catches at different times of the day in the case of Diptera and Hymenoptera, with the exception of some downward trend of the number in the tree stratum during late summer, and the late afternoon increase in the number of Diptera during July that possibly indicates some lateral movement of these insects into the station at that time. The evidence for a seasonal influence upon the catches of Cicadellidae is more marked. The shrub-wise movement at noon during the summer seems to show a movement into a stratum that was more moderate with respect to physical factors.

TABLE 5. The stratal differences in abundance of Cicadellidae for different hours (monthly means).

Month	Name of Strata	Average Number of Animals		
		Morning	Noon	Late Afternoon
April, 1932	Herbs	16.0	23.2	16.0
	Ground	204.6	72.6	176.0
	Dev.	−188.6	− 49.4	−160.0
	Trees	101.6	140.0	81.6
	Ground	204.6	72.6	176.0
	Dev.	−103.0	+ 67.4	− 94.4
May, 1932	Shrubs	12.0	11.0	9.0
	Herbs	19.0	10.0	17.1
	Dev.	− 7.0	+ 1.0	− 8.0
	Trees	23.0	34.0	18.0
	Herbs	19.0	10.0	17.0
	Dev.	+ 4.0	+ 24.0	+ 1.0
June, 1932	Shrubs	5.0	14.0	7.0
	Herbs	7.0	6.0	12.0
	Dev.	− 2.0	+ 8.0	− 5.0
	Trees	24.0	19.0	10.0
	Herbs	7.0	6.0	12.0
	Dev.	+ 17.0	+ 13.0	− 2.0
July, 1932	Shrubs	16.0	28.0	19.2
	Herbs	33.6	12.8	24.8
	Dev.	− 17.6	+ 15.2	− 5.6
	Trees	72.8	41.6	39.2
	Herbs	33.6	12.8	24.8
	Dev.	+ 39.2	+ 28.8	+ 14.4
August, 1932	Shrubs	22.7	54.7	50.7
	Herbs	33.3	37.3	38.7
	Dev.	− 10.6	+ 17.4	+ 12.0
	Trees	118.7	50.7	52.0
	Herbs	33.3	37.3	38.7
	Dev.	+ 85.4	+ 13.4	+ 13.3
October, 1937	Herbs	48.0	33.8	60.4
	Ground	35.4	33.0	51.3
	Dev.	+ 12.6	+ 0.8	+ 9.1
	Trees	48.4	37.8	22.7
	Ground	35.4	33.0	51.3
	Dev.	+ 13.0	+ 4.8	− 28.6

SEASONAL FLUCTUATIONS

While it was not the purpose of this work to study seasonal changes in population other than in relation to possible diurnal movements, since the data were at hand, it was treated briefly to show some of these changes.

If ecologists knew more about the food and breeding habits of species collected in ecological studies the interpretation of many changes in the animal populations could be more satisfactorily made. Some insects are known to have two or more host plants on which they feed at different seasons. Among these are Cicadellidae and Aphididae. Two of the leafhoppers, well known because of the damage they often cause to cultivated crops, are *Empoasca mali* Le Baron and *Eutettix tenellus* Baker. According to Crosby and Leonard (1918), *Empoasca mali* is a common pest of the apple in the fall and early spring and migrates to potato in the summer where it often causes considerable damage. The adults move back to the apple in the fall and deposit the winter eggs there. The same writers state that *Eutettix tenellus* migrates in the late spring from its wild food plants (*Atriplex* sp., Russian thistle, and greasewood) and settles in fields of sugar beets where its eggs are usually deposited during the first half of July. Many of the injurious Aphididae have host plants for the winter different from those of the summer. Quaintance and Siegler (1922) state that *Eriosoma lanigerum* Hausm. feeds on apple trees throughout the year but winged females migrate to elm trees in the fall for egg laying. These eggs hatch in the spring and the aphids feed on the young foliage of the elm with a later generation migrating back to the apple trees. These are simply given as examples of the migrations some insects are known to make.

There seem to be certain fairly definite periods of the year during which insects of the forest are influenced in their movements by environmental or biotic factors or both. There is the premigratory period of early spring, commonly called the prevernal period; the vernal period, that is characterized by an abundance of migratory animals; the estival period, the early part of which is the time of reproduction of many forms; the autumnal or prehibernation period; and the hiemal or hibernation period.

In order to show some of the trends in population throughout the year, a series of graphs were made with the animals, collected in each stratum, plotted to scale. A few of the more common species are used to illustrate, along with the discussion of these graphs, some of the seasonal changes of species. The total animals, Diptera, Hymenoptera, and Cicadellidae were treated graphically by plotting the means of each day's collections for each stratum. These physical factors were also plotted to scale (Figs. 11-14): mean relative humidity, obtained by taking the average of the stratal means of relative humidity; mean temperature, similarly obtained from three readings taken on the days of collection for the dates plotted; mean weekly temperature, which was taken

from the means obtained from the maximum and minimum thermometer readings; and mean weekly evaporation, obtained by taking the mean of weekly evaporation by strata for the dates shown in the figures. The mean weekly temperature was not plotted in Figures 11 and 14 due to insufficient space but reference to Figures 12 and 13 will show the seasonal variations of temperature. The break in each curve is due to the fact that the study did not include the month of September.

A consideration of the seasonal variations of total animals (Fig. 11) shows considerable variation in the
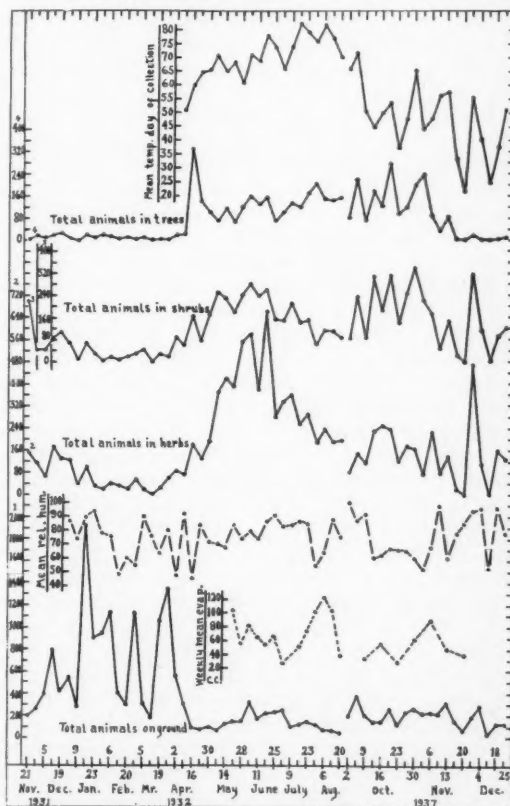
FIG. 11. Seasonal variations of total animals and certain physical factors.

number of animals on the ground from November 21, 1931, until April 16, 1932. This is largely determined by leafhopper variations in the catches for this period. The total population of the ground stratum decreased markedly from March 26 until April 16. There was, accordingly, an increase in the population of the upper strata with the peak of abundance on April 16 for the tree stratum. This change marked the premigratory movements of certain insects, principally leafhoppers, from the leaf mat in which they had been prominent during the winter. This prevernal period may be given approximately as March 19 until April 16. This was a period of gradually in-

creasing temperature and some increase in relative humidity due to rains the last week of March. These factors were evidently important in stimulating the movements of the animals at this time. The noticeable drop in the total population on April 23 was apparently due to the movement of the leafhoppers as many of them left this portion of the forest and probably migrated to nearby fields. This vernal migratory period ended about the middle of May at which time all of the migratory forms had apparently left the station. The mean weekly temperature was still increasing during this vernal period but the upward trend was not so marked as during the prevernal society and relative humidity showed less variation. The increase in the total population from April 23 was largely due to a considerable increase in the numbers of Diptera. These insects greatly influenced the total population curves of the upper strata during the early summer. The total animal population was larger in the herb stratum during the summer than in any other season of the year. The early part of the summer was characterized by increasing temperature and little change in relative humidity although the evaporation decreased, in general, from May 21 until July 2. This period, which ended in the present study about July 23, is commonly called the estival period and is the season of reproduction of many of the common forms found in the forest. Late summer was characterized by some decrease in the total population, probably due, in part, to a considerable drop in the numbers of Diptera. This portion of the summer, which is often separated from the early part and called the serotinal period, was characterized by uniformly high temperature, with a drop during the week ending August 20, and increasing evaporation until August 6 followed by a marked decline in evaporation until the last reading of the season, which was on August 20. The total population curves for the autumn show greater numbers of animals in the shrub and tree strata than were found in these strata during the summer. This was apparently caused by the influx of migrating species, among which the leafhoppers were prominent, from other habitats. This increase of migrating species during the autumnal period seems to be related somewhat to the decrease in the mean weekly temperature due to cooler nights although other physical as well as biotic factors were probably important in stimulating this movement. Relative humidity was high during the first two weeks of October and evaporation was low until October 23. The population curves for the autumn are very irregular, possibly due to rains that interfered with many collections and to variations of temperature. The first killing frost of the season was on October 24 and from October 30 there was a general decline in the number of animals in the upper strata with the exception of a few species. An increase in evaporation from October 23 to November 6, together with the low minimum temperatures and the effect of autumn frosts on the vegetation, were probably all important factors related to this decrease in the num-

ber of animals. This autumnal or prehibernation period ended about the middle of November and the hiemal period following was characterized by inactivity of many of the animals, with only a few species of insects and spiders showing activity on warm days. Aphids (*Myzocallis* n. sp.? and *Callipterini* sp.) were particularly abundant in the shrub and tree collections on October 20, October 30, November 3, and November 13, while the high peak of the curves of the herb and shrub strata on November 27 was largely due to an abundance of *Ptenothrix* sp. in the collections. The latter were also rather abundant in the herb and shrub collections of December 4, 18, and 25.

There was an increase in the number of Diptera (Fig. 12) caught in all of the upper strata from April 9 with peaks of abundance on May 14, May 28, June 18, and July 23. These insects decreased considerably after July 23. That is, the Diptera were most abundant in the vernal and estival periods that were characterized by increasing mean weekly temperature, a moderate evaporation, and no marked fluctuations of relative humidity. The decrease in late summer (serotinal period) accompanied uniformly high temperature and evaporation during late July and a decrease of these factors in
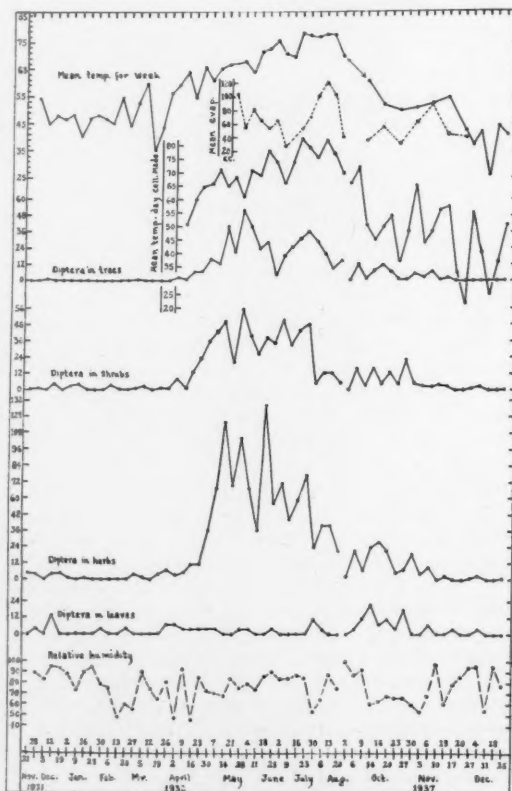
Fig. 12. Seasonal variations in numbers of individual Diptera and certain physical factors.

August. The herb stratum contained the greatest number of Diptera throughout the summer with the exception of July 30 when there were 5 more per square meter in the tree stratum. This superiority of numbers in the herb stratum was most marked from May 14 until June 18. Most species of Diptera were present only in the summer collections but some species appeared also in the collections during other seasons. Among these were: *Mycetophila punctata* Meig., *Sciara petaini* (Pettey), *Megaselia* sp. (prob. *scalaris* Lw.), *Chloropisca glabra* (Mg.), *Lucilia* sp., *Scatophaga stercoraria* (L.), and *Atrichopogon* sp. All of these species were present in the summer collections and their presence during other seasons are noted below. *Mycetophila punctata* and *Scatophaga stercoraria* were collected from the ground during the hiemal and prevernal periods. *Sciara petaini, Chloropisca glabra,* and *Megaselia* sp. were collected occasionally in the autumnal period. The following are the more common species of Diptera collected only in the autumnal or the early hiemal period: *Diplosis* sp., *Cladura flavorferruginea* O. S., *Trichocera* sp., *Boletina* sp., *Rhamphomyia* sp., *Psychoda interdicta* Dyar, and *Drosophila* sp. They probably migrated, preparatory to hibernation, into the more sheltered forest as environmental factors changed.

Hymenoptera (Fig. 13) occurred in some abundance in the spring and summer collections from April 2 until August 20 and in the autumn collections until October 30. As in the case of Diptera, they were most common in the herb collection. The peaks of abundance in the herb, shrub, and tree strata did not coincide so regularly as those of the Diptera. It seemed likely that the stratal variations in the numbers of Hymenoptera and Diptera were caused, to a considerable extent, by the seasonal change in the abundance of different species since no apparent relations were observed between these stratal variations and variations of physical factors. Nor could any apparent relation be observed between the seasonal variations of Hymenoptera and seasonal changes of physical factors. These insects were present, in some abundance, in the collections of all seasons except the winter season although many of the species collected in the autumn were not taken during the summer. A complete list of the species is given in the appendix and only a few species will be considered here. Many of the species occurred only in the summer collections but some were taken in the autumn as well. Among the species collected in the estival, serot'nal, and autumnal periods were: *Leptacis americana* (Ashm.), *Chrysocharis* sp., *Aspilota* sp., *Apanteles* sp., and *Aperileptus* sp. *Aspilota* sp. was also collected on December 19, 1937. The following are some of the species which were collected only in the autumnal period: *Omphale bicincta* Ashm., *Microterys cincticornis* Ashm., *Anagrus epos* Gir., *Rogas nolophanae* Ashm., *Meteorus* sp., and *Phaeogenes* sp.

Seasonal changes of the Cicadellidae are shown in Figure 14. Nymphs were not used in the preparation of this figure since it was considered unlikely that an adequate sampling could be made of leafhoppers at
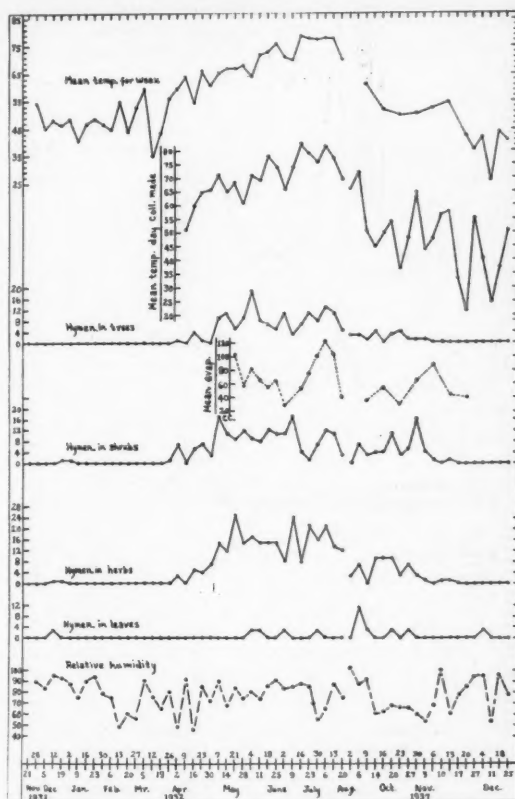
FIG. 13. Seasonal variations in numbers of individual Hymenoptera and certain physical factors.

this stage of the life cycle. DeLong (1932) regards it as almost impossible to get accurate information concerning nymphal populations of leafhoppers by the sweep method. The leafhoppers decreased in the collections from the herb and shrub strata from November 21 until November 28, 1931, and increased in the collections from the ground on November 28. They were found in the leaf mat in great abundance throughout the winter with larger catches usually occurring on warm days since they apparently moved up into the leaf mat more on such days. Some marked variations in the numbers caught on different days were also due to the difference in the thickness of the leaf mat in different parts of the station. An example of this is in the collection of January 16. On this date, the leafhoppers were collected from a thick cover of large, dry sycamore and oak leaves under which they were aggregated in considerable numbers. As noted in the discussion of the total population, the last day of abundant collections of these insects from the ground was on March 26 and they dropped rapidly in this stratum until April 16. Accordingly, there were increases of these insects in the herb and shrub strata from March 26 and in the tree stratum from April 2. They reached a peak of

FIG. 14. Seasonal variations in numbers of individual Cicadellidae and certain physical factors.

cincta Fh., *Erythroneura comes* Say, *Erythroneura vulnerata* Fh., *Hymetta distincta* Fairb., and *Graphocephala versuta* (Say). Leafhoppers were abundant in the first collections made in the upper strata during the early autumn although they appeared in the collections of the ground stratum on October 9 and were fairly abundant in these collections by October 27. The physical factors, as related to this movement, have been given in the paragraph dealing with the autumnal changes of the total population. The leafhoppers which were abundant in the prevernal and vernal periods reappeared in the collections of the autumnal period. However, these insects were not so abundant in the fall and early winter of 1937 as in the winter season of 1931-1932.

The increasing temperature of the prevernal and vernal periods with the beginning of the development of vernal foliage were probably important factors in stimulating the movements of the animals during these periods. The lower number of animals during the estival period was apparently due to the absence of the migrating species and to the presence of many summer residents in stages of the life cycle not readily obtained in the sweepings. The serotinal period was characterized particularly by an increase in the number of Cicadellidae and a decrease in the number of Diptera. The development of young leafhoppers was evidently hastened by the hot, dry weather that characterized the early part of this period. The increase in the number of animals during the autumn was evidently largely due to an influx of migrating species which were probably influenced by the lower temperatures' at night and other physical and biotic factors.

STRATAL DISTRIBUTION OF ANIMALS

Having studied the data for evidences of diurnal vertical movements of the animals, it seems important to consider the stratal gradients of physical factors and to study the stratal distribution of the species collected in relation to these.

The averages of the mean temperatures for the morning, noon, and late afternoon readings (Table 6) and the averages of the mean temperatures obtained from the maximum and minimum thermometers (Table 7) show a somewhat greater gradient of temperature between the herb and shrub strata than between the ground and herb strata with the gradient least from the shrubs to the trees. However, a consideration of the means of the mid-day temperatures alone (Table 6) shows a greater temperature gradient from the ground to the herbs than from the herbs to the shrubs.

The averages of the mean percentages of relative humidity (Table 8 and Table 9) show a greater gradient of relative humidity from the ground to the shrub stratum than from the shrub to the tree stratum, that is, there was a greater gradient within 3 feet of the ground.

The difference of mean evaporation (Fig. 15, Table 10) was least between the herb and shrub strata

abundance in the herbs on April 9 and in the trees on April 16. The curves clearly indicate this upward movement from April 2 with the population wave passing the herbs first and the trees last. The curve for the leafhopper population of the tree stratum drops until May 7. This apparently marked the end of their vernal migratory movements. The meteorological conditions that accompanied these movements were given in the discussion of the prevernal and vernal changes of the total population. The following were abundant migrating species: *Erythroneura noevus* (Gill.), *Erythroneura obliqua* Say, and *Empoasca* sp. These were absent in the summer collections of the station with the exception of a few dates in late summer and only a few specimens were caught on those dates. The species common in the collections of the summer were not found in any great numbers from May 7 until June 25. The latter date marked the beginning of an increase in the numbers in the tree collections with increases following in the shrub and herb strata in the order named. This increase was evidently due, in part, to the maturing of nymphal forms of the species which did not migrate from the station. The most common of these species were: *Erythroneura vitis* Harr., *Erythroneura tri-*

TABLE 6. Temperatures (°F.) as recorded in the different strata.

Date	Under Leaves			On Leaves			Herbs 1.5 feet			Shrubs 3 feet			Trees 25 feet		
	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening
1932															
Apr. 9	47	52	53	46	54	53	45	53	54	45	52	54	44	51	54
Apr. 16	48	70	58	46	73	60	46	70	62	46	70	64	49	70	65
Apr. 23	60	64	64	62	66	64	62	67	66	62	66	66	64	68	68
Apr. 30	61	70	62	61	67	63	60	71	66	60	70	67	60	70	70
May 7	62	76	69	62	78	70	60	82	71	60	83	72	63	84	74
May 14	56	70	64	54	72	64	52	74	67	52	76	68	54	77	70
May 21	62	70	66	62	71	66	62	76	68	62	78	68	64	79	68
May 28	60	64	60	58	64	60	56	66	60	56	66	60	56	67	60
June 4	65	72	70	65	73	71	65	74	72	65	76	72	66	79	74
June 11	64	70	68	64	72	69	65	73	70	65	73	70	66	76	72
June 18	70	80	76	72	80	76	72	84	79	72	85	80	74	90	82
June 25	76	78	71	71	78	72	70	80	73	70	80	72	72	81	74
July 2	62	70	67	62	72	66	66	79	76	65	80	76	66	84	79
July 9	68	76	72	67	76	74	66	78	76	65	80	76	66	84	79
July 16	76	85	80	76	85	80	76	88	83	76	88	84	77	92	86
July 23	74	82	78	74	82	78	72	84	80	72	84	80	74	87	81
July 30	68	78	76	68	77	76	68	78	76	66	78	78	68	80	80
Aug. 6	70	88	81	71	86	81	70	90	85	69	90	86	71	92	88
Aug. 13	72	80	76	72	80	72	72	84	76	72	84	75	72	86	76
Aug. 20	61	72	72	60	73	72	56	77	74	56	77	74	56	79	76
1937															
Oct. 2	61	66	67	61	66	67	61	66	68	61	66	68	62	68	68
Oct. 6	66	73	71	66	74	72	65	76	74	65	76	74	66	82	76
Oct. 9	52	52	54	52	52	54	52	50	50	48	50	51	48	50	50
Oct. 14	45	48	47	44	49	47	39	48	46	39	48	45	39	49	44
Oct. 16	43	52	53	41	54	54	37	56	56	38	57	56	38	58	56
Oct. 20	51	55	54	48	56	55	45	58	56	45	58	56	45	62	58
Oct. 23	42	43	42	38	42	40	34	36	36	34	37	36	33	37	36
Oct. 27	46	48	50	44	50	51	41	50	51	41	51	51	42	52	50
Oct. 30	53	60	61	54	64	66	56	72	72	56	73	74	56	78	74
Nov. 3	46	48	47	42	47	46	36	46	46	37	48	45	37	48	45
Nov. 6	45	49	48	41	50	48	38	54	50	38	56	52	38	57	52
Nov. 10	54	56	58	54	57	58	53	58	59	54	58	59	53	58	59
Nov. 13	52	56	51	52	58	52	52	64	58	52	65	58	52	67	61
Nov. 17	38	40	38	34	36	33	30	32	32	30	33	32	30	32	32
Nov. 20	30	32	33	24	40	38	17	25	23	18	25	23	18	24	22
Nov. 27	49	54	54	52	57	56	53	58	58	54	58	58	54	58	58
Dec. 4	39	42	42	38	42	42	38	42	40	38	42	41	38	42	41
Dec. 11	24	27	30	18	24	26	13	28	28	14	28	29	14	30	30
Dec. 18	42	42	42	38	40	39	35	36	36	36	37	36	36	37	35
Dec. 25	44	48	48	43	50	49	44	56	54	44	56	56	44	56	56
Mean	55.0	61.5	59.3	53.9	62.2	59.5	52.3	63.3	60.5	52.5	63.8	60.8	52.9	65.3	61.7
Stratal Ave...	58.6			58.5			58.7			59.0			60.0		

Dropped .5 on even number; added .5 on odd numbers.

TABLE 7. Maximum and minimum temperatures (°F.) in the different strata as recorded weekly in 1931, and 1937 (calculated means are shown).

Week	Under Leaves			Herbs 1.5 feet			Shrubs 3 feet			Trees 25 feet		
	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum
Nov. 21-28 '31	63.5	53.5	43.5	76.5	54.3	32.0	76.5	54.3	32.0	76.5	54.8	33.0
Nov. 28-Dec. 5	56.0	46.5	37.0	61.0	43.5	26.5	61.0	43.5	26.5	62.5	47.5	32.5
Dec. 5-12	62.5	47.5	32.5	65.0	47.5	30.0	64.5	47.0	29.5	66.0	50.8	35.5
Dec. 12-19	61.5	49.8	38.0	64.0	45.0	26.0	63.5	44.8	26.0	66.0	46.5	27.0
Dec. 19-26	59.5	52.5	45.5	66.5	52.5	38.5	72.5	55.8	39.0	74.5	56.8	39.0
Dec. 26-Jan.2 '32	56.5	47.3	38.0	67.5	48.8	30.0	67.5	48.5	29.5	68.0	49.3	30.5
Jan. 2-9	51.5	43.3	35.0	54.0	36.5	19.0	54.0	40.3	26.0	55.5	41.3	27.0
Jan. 9-16	59.5	46.0	32.5	71.5	47.0	22.5	71.5	46.8	22.0	72.0	47.0	22.0
Jan. 16-23	59.5	47.3	35.0	69.0	48.5	28.0	70.5	49.0	27.5	70.0	49.0	28.0
Jan. 23-30	59.5	47.3	35.0	67.0	46.8	26.5	66.5	46.0	25.5	68.5	46.8	25.0
Jan. 30-Feb. 6	63.5	47.0	30.5	66.0	44.0	22.0	66.0	43.8	21.5	66.5	43.8	21.0
Feb. 6-13	61.5	50.5	39.5	76.5	55.3	34.0	83.5	59.3	35.0	80.0	57.3	34.5
Feb. 13-20	56.0	45.5	35.0	59.0	44.0	29.0	58.5	43.5	28.5	59.0	43.5	28.0
Feb. 20-27	57.5	46.8	36.0	77.5	53.5	29.5	78.5	53.5	28.5	85.0	57.3	29.5
Feb. 27-Mar. 5	67.5	56.0	44.5	79.5	60.0	40.5	81.5	61.0	40.5	81.0	61.0	41.5
Mar. 5-12	59.5	45.5	31.5	57.5	31.8	12.0	48.5	29.3	10.0	49.0	29.5	10.0
Mar. 12-19	64.5	45.5	26.5	70.5	42.0	15.0	73.5	43.3	13.0	72.0	42.5	12.0
Mar. 19-26	73.5	54.3	35.0	83.5	56.0	28.5	86.3	57.0	28.0	87.5	58.0	28.5
Mar. 26-Apr. 2	75.5	56.3	37.0	86.5	59.5	32.5	89.5	61.3	33.0	88.0	60.0	33.5
Apr. 2-9	82.0	63.8	45.5	88.0	55.0	42.0	85.5	65.0	41.5	85.0	63.0	41.0
Apr. 9-16	78.5	58.5	39.0	77.1	53.0	34.5	73.0	53.8	34.5	71.5	53.0	34.0
Apr. 16-23	96.5	70.5	44.5	90.5	65.0	39.5	92.0	65.5	39.0	86.0	63.0	40.5
Apr. 23-30	84.0	64.3	44.5	82.5	59.5	36.5	83.5	59.8	36.0	83.0	59.8	36.5
Apr. 30-May 7	81.5	66.5	51.0	85.5	64.5	43.5	89.0	56.8	42.5	88.0	65.5	42.5
May 7-14	79.5	66.8	54.0	84.5	67.0	49.5	86.5	67.3	48.0	86.0	67.3	48.5
May 14-21	76.5	66.5	56.0	80.5	66.0	51.5	83.5	67.3	51.5	85.5	69.5	53.5
May 21-28	75.5	66.8	58.0	80.0	68.0	55.5	81.5	68.3	55.0	84.0	69.5	55.0
May 28-June 4	76.5	64.3	52.0	81.5	63.0	44.5	82.5	63.3	44.0	86.5	65.3	44.0
June 4-11	77.5	70.0	62.5	84.0	72.0	60.0	85.0	71.5	58.0	88.0	73.5	59.0
June 11-18	79.5	71.0	62.5	85.5	72.8	60.0	86.5	72.8	59.0	89.5	74.5	59.5
June 18-25	82.5	74.5	66.5	87.5	76.5	65.5	88.0	75.8	63.5	92.0	78.0	64.0
June 25-July 2	79.5	71.0	62.5	82.5	70.3	58.5	83.5	70.3	57.0	87.0	72.3	57.5
July 2-9	78.5	70.5	62.5	80.0	69.8	59.5	81.0	69.8	58.0	84.0	71.5	59.0
July 9-16	85.0	77.5	70.0	87.5	78.5	69.5	88.5	78.3	68.0	92.0	80.3	68.5
July 16-23	85.5	77.5	69.5	88.0	77.8	67.5	89.0	78.0	67.0	92.0	79.8	67.5
July 23-30	88.5	77.8	67.0	88.5	76.5	64.5	90.0	77.0	64.0	93.0	78.0	65.0
July 30-Aug. 5	90.5	78.5	66.5	90.5	77.5	64.5	91.5	77.8	64.0	94.0	79.8	65.5
Aug. 6-13	88.0	77.5	66.5	91.5	77.8	64.0	92.0	77.8	63.5	94.0	78.5	64.5
Aug. 13-20	81.5	71.0	60.5	83.5	69.8	56.0	84.0	69.0	55.0	85.5	71.3	56.0
Oct. 2-9, 1937	73.5	61.3	49.0	77.0	59.5	42.0	77.5	60.0	42.5	82.0	62.0	42.0
Oct. 9-16	36.0	52.5	39.0	68.5	50.5	32.5	69.5	51.0	32.5	72.5	52.8	33.0
Oct. 16-23	32.5	51.5	40.5	66.0	49.0	33.2	37.0	19.8	32.5	68.5	50.5	32.5
Oct. 23-30	31.0	49.5	37.5	73.0	49.8	26.5	74.5	51.0	27.5	78.5	52.5	26.5
Oct. 30-Nov. 6	33.0	51.0	39.0	75.0	51.8	28.5	76.0	52.0	29.0	81.0	55.0	29.0
Nov. 6-13	38.0	51.3	44.5	66.0	54.0	42.0	36.0	36.3	16.5	18.5	56.5	44.5
Nov. 13-20	56.0	42.5	29.0	66.5	41.8	17.0	68.0	42.9	17.8	57.0	43.2	19.5
Nov. 20-27	54.0	40.3	26.5	58.5	35.8	13.0	59.0	36.5	14.0	59.0	36.8	14.5
Nov. 27-Dec. 4	54.5	42.5	30.5	57.5	40.8	24.0	59.0	42.0	25.0	42.8	25.5	
Dec. 4-11	43.0	32.3	21.5	40.5	22.8	5.0	42.0	24.0	6.0	42.0	25.8	9.0
Dec. 11-18	57.5	42.0	26.5	64.0	43.3	22.5	34.5	15.0	25.5	60.5	45.3	25.5
Dec. 18-25	49.5	39.8	30.0	57.0	40.8	24.5	56.5	41.0	25.5	59.0	44.0	29.0
Stratal Average	56.6			55.9			56.2			57.3		

although the evaporation gradient decreased rapidly from the shrub to the tree stratum. That is, the evaporation gradient was much greater within 3 feet of the ground. An animal moving upward would pass into a region of approximately twice the evaporating power of the air from the ground to the herb stratum, of more than twice the evaporating power of the air from the ground to the shrub stratum, and of more than three times the evaporating power of the air in passing from the ground to the tree stratum.

Light readings (Fig. 16, Tables 11, 12) were only taken on two days because of the difficulty of making quick accurate readings at the time of each collection. These days (May 3 and July 31) were selected as representative days before the foliage was well developed and after full foliage development. Figure 16, A, shows the greatest amount of light at 10:50 a.m. on May 3 and Figure 16, B, shows this peak to be at 2:20 p.m. in the trees and 3:40 p.m. in the lower strata on July 31. The light gradient was greatest near the ground and fell rapidly above the shrub stratum.

This seems to show that there are very definite

TABLE 8. Relative humidity (% RH) as recorded from wet and dry bulbs during the early morning, at noon and in the late afternoon (readings corrected).

Date	Two inches above surface			Herbs 1.5 feet			Shrubs 3 feet			Trees 25 feet		
	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening
1937												
Oct. 2	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	99.0	100.0	100.0
Oct. 6	100.0	89.0	95.0	97.0	83.0	89.0	97.0	79.0	82.0	93.0	64.0	76.0
Oct. 9	90.0	93.5	94.0	90.0	87.0	94.0	93.0	87.0	94.0	93.0	93.0	93.0
Oct. 14	88.0	55.0	56.0	84.0	45.5	47.0	84.0	35.0	52.5	88.0	36.5	50.0
Oct. 16	87.5	54.5	66.0	91.0	39.5	56.0	87.0	38.0	53.0	87.0	36.5	45.5
Oct. 20	89.0	82.5	76.5	86.0	52.5	63.5	86.0	57.5	55.5	72.5	46.5	39.5
Oct. 23	81.5	62.5	69.0	81.5	57.0	65.0	80.0	50.0	60.0	80.0	49.0	59.0
Oct. 27	88.0	62.0	63.0	88.0	53.0	58.0	84.5	54.0	57.0	84.5	49.0	54.0
Oct. 30	82.0	61.0	54.0	77.0	59.5	50.0	77.0	54.0	44.0	67.5	44.0	50.5
Nov. 3	80.0	46.0	50.0	79.0	38.0	44.0	71.0	36.0	40.0	70.0	33.0	39.0
Nov. 6	92.0	61.5	69.0	92.6	46.5	66.0	91.5	44.0	63.0	84.0	40.5	60.0
Nov. 10	97.0	100.0	100.0	97.0	97.0	97.0	97.0	97.0	97.0	97.6	97.0	97.0
Nov. 13	94.0	66.0	45.5	91.0	58.0	41.5	91.0	45.0	32.0	88.0	42.0	28.0
Nov. 17	95.0	79.5	76.5	89.0	79.0	79.0	78.5	74.0	74.0	73.5	74.0	66.0
Nov. 20	94.0	87.0	94.0	84.5	74.5	93.5	84.0	74.0	89.5	84.0	68.0	89.5
Nov. 27	97.0	97.0	94.0	97.0	94.0	91.5	97.0	91.0	91.0	97.0	91.0	89.0
Dec. 4	96.0	96.0	96.0	96.0	96.0	96.5	96.0	96.0	96.0	96.0	96.0	96.0
Dec. 11	82.0	63.5	66.0	81.0	47.0	50.5	72.5	26.0	45.0	50.0	23.0	34.0
Dec. 18	98.0	98.0	95.5	97.0	97.5	93.0	97.5	96.0	93.0	95.0	95.5	93.0
Dec. 25	93.0	84.0	76.0	89.0	76.0	70.5	89.0	73.0	66.0	86.0	70.0	63.5
Mean	91.2	76.9	76.8	89.4	69.0	72.3	87.7	65.4	69.2	84.2	62.4	66.1
Stratal Average	81.6			76.9			74.1			70.9		

TABLE 9. Relative humidity as recorded from hair hygrometer readings during the early morning, at noon and in the late afternoon (readings corrected).

Date	On Leaves			Herbs 1.5 feet			Shrubs 3 feet			Trees 25 feet		
	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening	Morning	Noon	Evening
1932												
Feb. 13	71.0	45.0	33.5	71.5	43.0	32.5	69.0	41.0	32.5	62.0	37.0	34.5
Feb. 20	87.0	55.0	41.5	85.5	53.0	42.5	83.5	51.5	43.5	78.5	49.0	44.0
Feb. 27	90.0	44.5	38.5	88.0	45.0	37.0	84.0	45.0	35.0	77.0	43.5	30.0
Mar. 5	97.0	82.0	96.0	96.0	82.5	95.5	93.0	83.0	94.0	92.0	78.5	94.0
Mar. 12	91.0	76.5	71.5	85.0	74.5	70.5	84.0	73.5	68.5	78.0	73.5	68.5
Mar. 19	97.0	51.0	55.0	96.0	51.0	51.0	93.0	51.5	43.0	86.0	52.0	41.0
Mar. 26	71.0	84.0	95.0	67.0	84.0	95.5	62.0	80.0	97.0	59.0	66.0	97.0
April 2	78.0	39.0	46.0	74.0	36.0	41.5	66.0	32.0	34.0	60.0	29.0	28.5
April 9	96.0	94.0	95.0	95.0	90.0	93.0	96.5	87.0	91.0	93.0	82.0	88.0
April 16	66.0	35.0	37.5	65.5	33.5	38.0	63.0	32.0	37.5	57.5	32.0	38.0
April 23	87.0	92.5	87.0	82.0	92.5	85.5	81.0	90.0	82.5	74.0	81.5	75.5
April 30	100.0	73.5	55.0	100.0	64.0	53.0	99.5	60.5	51.0	97.0	53.5	52.0
May 7	83.0	61.0	59.5	84.0	52.0	58.0	86.0	47.0	56.5	83.0	44.0	50.0
May 14	95.0	59.0	68.0	93.0	57.0	63.5	94.0	49.0	56.0	80.0	46.0	50.0
May 21	99.0	84.5	87.5	97.0	80.5	81.5	95.0	73.0	76.0	87.0	65.5	77.5
May 28	86.0	82.0	74.5	82.0	78.0	70.0	79.0	75.0	75.0	65.0	73.0	66.0
June 4	89.0	87.0	83.5	83.5	82.5	77.0	82.0	80.0	73.0	75.5	68.0	66.0
June 11	82.5	81.0	77.0	77.5	78.5	72.0	70.0	71.0	68.0	68.0	63.0	63.0
June 18	96.5	89.0	85.0	96.0	88.5	83.5	93.0	84.0	81.0	83.5	72.0	77.5
June 25	91.0	87.0	99.0	88.5	87.0	100.0	86.0	85.0	100.0	87.0	79.5	100.0
July 2	94.0	82.0	96.0	91.5	76.5	91.5	91.5	70.5	87.0	79.0	61.0	77.5
July 9	98.0	85.5	90.0	96.5	77.0	87.0	95.0	73.0	85.0	84.5	61.0	78.0
July 16	99.0	90.0	84.0	98.0	88.5	79.0	96.5	87.0	77.0	91.0	83.5	71.5
July 23	96.0	83.5	87.0	93.5	82.5	84.0	93.0	82.0	83.0	87.0	75.5	77.5
July 30	69.0	54.5	52.5	67.0	52.0	49.5	64.5	50.0	41.5	60.5	48.0	38.5
Aug. 6	79.5	72.0	51.5	81.5	70.0	49.0	76.5	64.0	43.0	66.0	67.0	42.0
Aug. 13	97.5	78.5	99.0	96.0	77.5	98.5	95.0	72.0	98.0	85.0	65.0	89.0
Aug. 20	95.0	79.5	69.5	94.0	70.5	65.0	94.0	66.5	61.5	87.5	64.0	50.5
Mean	89.3	72.4	72.0	86.6	69.6	69.4	84.5	66.3	66.8	78.0	61.2	63.1
Stratal Ave.	77.9			75.2			72.5			67.4		
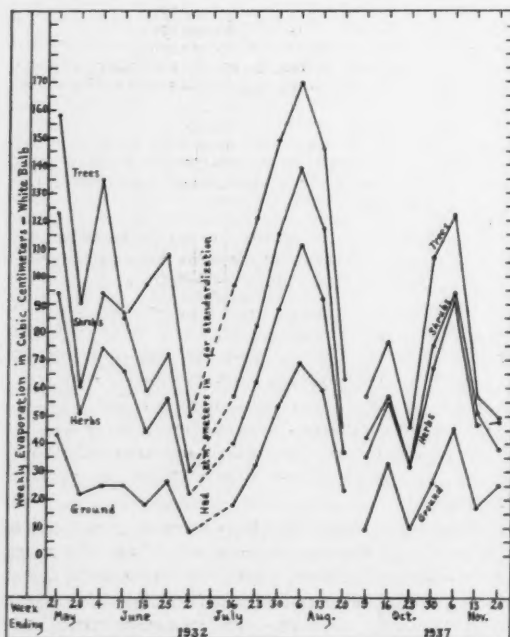
FIG. 15. Weekly evaporation in cubic centimeters in various strata during the summer of 1932 and the fall of 1937.

stratal differences of these physical factors with the greatest gradient near the ground and decreasing upward. The differences were least between the herb and shrub strata since the gradients of physical factors decreased upward and the distance between these two strata was the same as between the ground and herb strata.

Although biotic factors were not considered in the collection of the data, they probably greatly influenced the stratal distribution of many of the animals. It may be true that certain insect groups, as Hemiptera and Coleoptera, are affected largely in their stratal distribution by their food and it seems that many of the species of Hymenoptera would be present in the strata in which the animals they parasitize were feeding. Weese (1924) found that among the web-building spiders the mechanical features of the environment were of considerable importance, as well as environmental factors, in determining their horizontal and vertical distribution. Elton (1927) gives an illustration of a spider (Leptyphantes sobrius) which is always found in patches of stones, in stream gullies, or on the shores of ponds, lakes, or seas where the soil is very unstable. This condition of the habitat seems to be a definite factor always associated with the distribution of this spider.

TABLE 10. Weekly evaporation in cubic centimeters in the different strata during the summer of 1932 and fall of 1937.

Week	Leaf Mold Black	White	Excess of Black	Herbs—1.5 feet Black	White	Excess of Black	Shrubs—3 feet Black	White	Excess of Black	Trees 25 feet Black	White	Excess of Black
1932												
May 14-21..	46.8	43.3	3.5	98.8	94.4	4.4	120.1	123.0	-2.9	160.0	158.0	2.0
May 21-28..	23.4	22.0	1.4	54.3	51.2	3.1	62.4	61.5	0.9	98.4	90.7	7.7
May 28-June 4..	46.8	25.3	21.5	78.6	73.6	5.0	95.9	94.3	1.6	136.0	134.5	1.5
June 4-11..	39.0	25.1	13.9	72.1	65.6	6.5	83.5	86.9	-3.4	84.8	85.2	-0.4
June 11-18..	25.7	18.2	7.5	48.6	44.0	4.6	60.6	59.0	1.6	100.0	97.2	2.8
June 18-25..	28.1	26.6	1.5	62.4	56.0	6.4	71.0	72.2	-1.2	110.4	107.7	2.8
June 25-July 2*..	10.9	8.4	2.5	25.1	22.4	2.7	32.0	30.0	1.7	60.0	50.2	9.8
July 9-16..	27.3	17.5	9.8	45.4	40.0	5.4	52.3	51.7	0.6	100.0	97.2	2.8
July 16-23..	39.8	31.9	7.9	68.0	61.6	6.4	78.0	82.0	-4.0	120.0	120.7	-0.7
July 23-30..	62.0	53.2	8.8	90.7	88.0	2.7	96.7	114.8	-18.1	154.4	149.0	5.4
July 30-Aug. 6..	80.3	69.2	11.1	122.3	110.4	11.9	130.3	139.4	-9.1	169.6	170.1	-0.5
Aug. 6-13..	62.4	59.3	3.1	97.2	92.0	5.2	102.2	117.3	-15.1	145.6	145.8	-0.2
Aug. 13-20..	21.1	22.8	-1.7	37.3	36.0	1.3	46.0	36.9	9.1	65.6	62.8	2.8
1937												
Oct. 2-9..	7.3	8.9	-1.6	30.4	42.0	-11.5	34.9	34.9	-0.4	71.4	56.6	14.8
Oct. 9-16..	37.3	32.8	4.5	58.1	56.8	1.3	57.3	55.4	1.9	79.7	77.1	2.6
Oct. 16-23..	12.6	10.1	2.5	24.5	31.2	-6.7	27.0	31.6	-4.6	54.8	46.3	8.5
Oct. 23-30..	23.5	26.3	-2.8	66.4	66.7	-0.3	74.7	75.4	-0.7	105.4	107.0	-1.6
Oct. 30-Nov. 6..	42.9	46.2	-3.3	90.9	93.6	-2.7	102.5	94.3	8.2	123.7	122.2	1.5
Nov. 6-13..	20.3	16.6	3.7	49.0	50.7	-1.7	53.1	47.2	5.9	51.1	57.0	-5.9
Nov. 13-20.		25.1		39.5	38.2	1.3	49.0	48.4	0.6	52.3	49.2	3.1
Mean......	34.6	29.4		63.0	60.7		71.5	72.8		102.2	99.2	

*No records from July 2-9. Atmometers were being restandardized.

TABLE 11. Diurnal variations in light intensity as measured with MacBeth Illuminometer before full foliage development.

Time	Light Intensity in Foot Candles Ground	Herbs 1.5 feet	Shrubs 3 feet	Trees 25 feet
May 3, 1932				
4:50- 5:20 a.m......	1.7	3.0	9.3	27.9
5:30- 6:00 "	10.5	18.5	26.7	54.6
6:10- 6:40 "	24.3	32.8	47.3	87.3
6:50- 7:20 "	36.4	39.4	69.8	92.2
7:30- 8:00 "	41.2	55.8	87.3	109.2
8:10- 8:40 "	44.9	72.8	99.5	155.3
8:50- 9:20 "	82.5	87.3	145.6	206.2
9:30-10:00 "	84.9	112.8	157.7	182.0
10:10-10:40 "	97.0	128.6	182.0	182.0
10:50-11:20 "	127.4	169.8	198.6	221.9
11:30-12:00 "	104.0	143.1	192.7	192.7
12:10-12:40 p.m......	101.6	151.8	186.9	163.5
12:50- 1:20 "	99.3	111.0	169.4	151.8
1:30- 2:00 "	104.0	125.6	160.6	198.6
2:10- 2:40 "	125.6	116.8	128.5	146.0
2:50- 3:20 "	98.1	87.6	116.8	107.5
3:30- 4:00 "	75.9	72.4	75.9	81.2
4:10- 4:40 "	57.0	52.4	69.1	61.9
4:50- 5:20 "	35.2	35.8	42.5	52.2
5:30- 6:00 "	25.5	22.1	23.1	25.5
6:10- 6:40 "	5.0	4.0	2.5	1.8
Mean..........	65.8	78.3	104.4	119.1
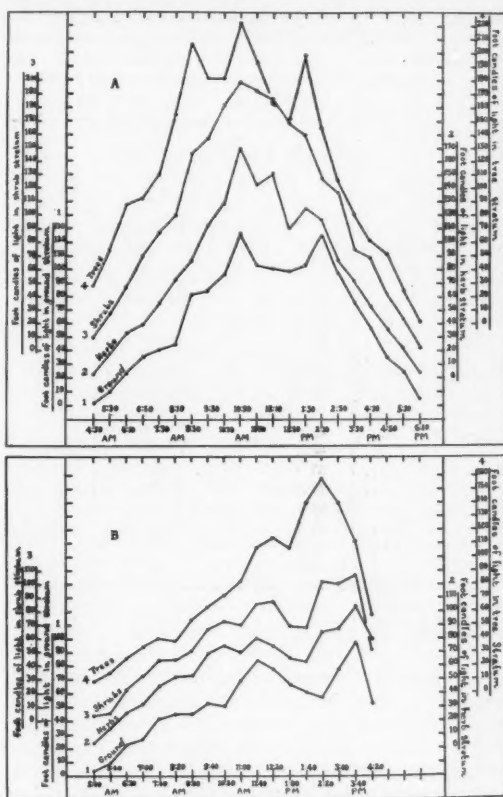
FIG. 16. Diurnal variations of light intensity in various strata as measured on two representative days. A, May 3; B, July 31.

Some of the more abundant species of animals were selected for a study of their stratal distribution and are treated briefly.

The most common species of leafhoppers in the tree stratum, other than at times of migration, were: *Erythroneura tricincta* Fh., *Erythroneura comes* Say, and *Erythroneura vulnerata* Fh. These species were occasionally taken from the herb and shrub strata at noon and in the late afternoon but not in any great numbers. *Graphocephala versuta* (Say) was commonly collected from both the herb and shrub strata. This does not indicate a lack of definite stratification, however, since this insect is common in shrubby vegetation and small shrubs were included in the herb stratum.

Hemiptera common in the collections were: *Lygus pratensis* L., *Euschistus tristigmus* Say, *Cryphula parallelogramma* Stal., *Allocoris agrella* McAtee, *Jalysus spinosus* Say, and *Hyaliodes vitripennis* (Say). *Lygus pratensis* and *Euschistus tristigmus* were hibernating species which occurred in the ground stratum during the winter. They were also taken in the herbs at that time and in the autumn while the latter was collected from the herbs and shrubs during

TABLE 12. Diurnal variations in light intensity as measured with MacBeth Illuminometer after full foliage development.

Time	Light Intensity in Foot Candles			
	Ground	Herbs 1.5 feet	Shrubs 3 feet	Trees 25 feet
July 31, 1932				
5:00- 5:30 a.m......	2.8	4.3	4.5	8.6
5:40- 6:10 "	9.6	14.5	5.5*	15.5
6:20- 6:50 "	23.1	26.1	23.3	26.1
7:00- 7:30 "	27.3	32.8	32.8	35.2
7:40- 8:10 "	42.5	46.0	44.9†	41.2†
8:20- 8:50 "	44.9	52.2	44.9	38.8
9:00- 9:30 "	44.9	53.4	51.0	54.6
9:40-10:10 "	53.4	69.1	66.7	63.1
10:20-10:50 "	51.0†	75.2	72.8	71.6
11:00-11:30 "	69.1	70.4	70.4	82.4
11:40-12:10 p.m.....	83.7	80.1	84.9	106.7
12:20-12:50 "	77.6	75.2	87.3	114.0
1:00- 1:30 "	65.5	65.5	69.1	106.7
1:40- 2:10 "	60.7	63.1	67.9	139.5‡
2:20- 2:50 "	57.1†	84.9	101.9	157.7
3:00- 3:30 "	77.6	87.3	99.5	139.5
3:40- 4:10 "	97.0	104.3	106.7	111.6
4:20- 4:50 "	53.4	80.1	52.2	58.2
Mean...........	52.3	60.3	60.4	76.2

*Cloud interference.
†Leaf interference.
‡Sun shining through trees.

the summer. *Cryphula parallelogramma* was collected principally from the ground stratum although it appeared occasionally in collections from the upper strata. *Jalysus spinosus* was taken principally in the herb stratum but appeared on a few dates in shrubs (April 16 and October 20) and the ground (December 5 and January 9) collections. *Allocoris agrella* was found largely in herb collections. It was taken from shrubs on April 16 and May 21 and probably hibernated on the ground in locations not examined. *Hyaliodes vitripennis* was common in the collections from all of the upper strata. According to Blatchley (1926), Uhler stated that they lived on wild grapevines as well as on red and black oaks where they searched for tender insects and larvae for food.

The stratal distribution of some of the abundant species of Diptera is given below. *Dicranoptycha winnemani* Alex., *Neophyllomyza* sp., *Sapromyza* sp., *Cladura flavoferruginea* O.S., and *Trichocera* sp. were collected almost entirely from the herb and shrub strata. *Minettia magna* Coq. and *Culicoides melleus* (Coq.) were collected from the shrub and tree strata although they occurred more often in the tree stratum. *Sciara petaini* (Pettey) and *Megaselia* sp. (prob. *scalaris* Lw.) were taken from all strata. They were common in the upper strata during the summer but appeared occasionally in ground collections during the summer and autumn. These species seemed to show some fairly definite stratal preferences and when collected from more than one stratum in the same season each species was more common in one stratum than in the other strata.

A few of the Hymenoptera are listed here by the strata in which they were caught. *Pteromalus* sp.

was taken from the ground and herb strata, *Euplectrus* sp. from the herbs only, *Platygaster* sp. and *Tetrastichus* sp. from the herb and shrub strata, *Rogas nolophanae* Ashm. from the shrubs only, and *Leptacis americana* (Ashm.) from the herbs, shrubs and trees although it was taken most often from the shrub stratum.

Some of the common Coleoptera were: *Baliosus ruber* (Weber), *Delphastus* sp., *Mordellistena* sp., *Apion turbulentum* Smith, *Melanophthalma distinguenda* Com., *Longitarsus solidaginis?* Horn, *Xanthonia* sp., *Diabrotica vittata* (Fab.) Auct., *Symphora rugosa* Hald., and *Microtonus sericans* Lec. *Baliosus ruber*, although not as common as the others, is given because it appeared only in herb collections with the exception of one tree collection (June 4). *Delphastus* sp. was taken principally in the shrub collections although this coccinellid was taken in tree collections on a number of dates and rarely from the herbs. Its distribution was probably due to the location of food for it evidently feeds on aleyrodids or other small, soft insects. *Apion turbulentum* was collected from the herb and shrub strata only. *Melanophthalma distinguenda* was commonly found in herb collections throughout the year and often in shrub sweepings. This species occasionally occurred in the tree collections but was evidently most common on the small shrubby plants. *Longitarsus solidaginis* was common in herb collections most of the year and was often found in shrub collections. *Mordellistena* sp. appeared in collections from the herbs, shrubs, and trees. It was found in the herb stratum as late as November 3 although no later than August 13 in the tree stratum. *Xanthonia* sp. was found principally in the shrub stratum but was taken in some abundance from the herb and tree strata in June and July. *Diabrotica vittata* appeared in all strata in April but was taken in tree collections later than in those from the other strata. This species was taken from the herbs and shrubs until the middle of June. It appeared in shrub collections October 2 and in collections from the herb stratum on October 9 but did not appear in collections from the ground until November 13. This indicates a downward movement for hibernation. *Symphora rugosa* was collected largely from the tree stratum. *Microtonus sericans* was found in shrub and tree collections and apparently came from the foliage of the elm trees many of which were young enough to have foliage within 3 feet of the ground.

Six species of spiders common in the collections were considered for their tendency to remain at certain levels. *Euryopis* sp. was taken almost entirely from the herb stratum although some were found in the leaf mat during the winter. This spider apparently made no web but showed a more definite stratification than most of the other non-web-building spiders collected in this study. *Synema parvula* Hentz was taken principally from the herb stratum although it appeared in the shrub collections occasionally from April until November 13. During the winter, it was taken largely in the herb stratum but appeared in ground collections on February 20 and

November 13. *Mangora placida* Hentz was commonly collected from the herb and shrub strata. Specimens were taken from the leaf mat on January 16. Young specimens appeared in herb collections during August. The web was made on low bushes. *Linyphia communis* Hentz was commonly found in both herb and shrub sweepings. It occurred in ground collections on April 9 and December 4. According to Comstock (1913), this species builds a bowl and doily web on bushes from quite near the ground to a height of 3 or 4 feet. *Anyphaena celer* (Hentz) was a very common species in herb sweepings throughout the year except in the collections of March, April, and May. The young appeared in June. This spider appeared in the shrub sweepings of June and was taken in low tree sweepings in the late summer and early autumn. This species was commonly found in rolled, dry leaves of *Eupatorium* sp. in the late autumn and early winter. It was collected from the ground, as well, throughout the winter and until April 9. This spider lives principally in silken tubes in rolled leaves of high herbs and shrubs. *Dictyna* sp. (prob. *foliacea* Hentz) was collected from all strata. It appeared in the vernal society of the upper strata and was found there until November 3. After that date it was taken in collections from the ground. Young forms appeared in the collections the last of July. This spider makes a web in a leaf that has been slightly rolled. There appeared to be no definite stratification of this species although it was taken less often in tree sweepings than in those from the herb and shrub strata.

It seemed that the spiders which do not build webs, but only make silken retreats in rolled leaves, as *Anyphaena celer* and *Dictyna foliacea*, were not so limited to certain strata as were those which build larger webs on tall herbs or shrubs. In the latter group are *Linyphia communis* and *Mangora placida*. The structural characters of the environment probably affected the stratification of the latter group greatly. Other spiders, as *Euryopis* sp. and *Synema parvula*, although they do not build webs, seemed to show definite stratal preference.

SUMMARY

1. There was, in general, an increase in the animal catches from morning until noon. Diptera increased more definitely in the noon catches of the shrub and tree strata than in the herb stratum. Cicadellidae increased more consistently in the noon catches of the shrub stratum than in the other strata. Hymenoptera and total animals increased more regularly in the noon catches of herb and shrub strata than in the tree stratum. These changes usually accompanied increases of temperature and decreases of relative humidity but apparently were not proportional to the variations of these factors.

2. In general, fewer animals were caught in the late afternoon collections than in the noon collections. Diptera, Cicadellidae, and total animals decreased more definitely in the shrub and tree strata with some gains in the herb stratum. Although these changes usually accompanied decreases of temperature and increases of relative humidity they apparently were not proportional to the changes of these factors.

3. The correlation coefficients indicate increases of animals with temperature increases, and decreases with temperature decreases in all strata, and, in general, increases of animals with relative humidity decreases, or vice versa, in all strata. However, this indicates little, if any, diurnal vertical movements since a positive correlation for the upper strata and a negative correlation for the lower strata would seem to be necessary to indicate any marked diurnal vertical movement.

4. The seasonal influence upon diurnal vertical movements, as considered from the monthly means of stratal collections of Diptera, Hymenoptera, and Cicadellidae, was not apparent for the first two groups of these insects although the general noon increases in all strata and the late afternoon decreases indicate some movement, possibly a lateral migration. A seasonal shrub-wise movement of Cicadellidae seemed apparent for the months June to August inclusive, as shown by the monthly mean stratal collections at noon.

5. Seasonal fluctuations were particularly marked during the vernal and autumnal periods. A pre-migratory movement occurred in the early spring with certain animals, among which the leafhoppers were prominent, moving from their places of hibernation up into the herb, shrub, and tree strata. This movement seemed to be associated with gradually increasing temperature and some increase of relative humidity. The migrating species apparently fed for a short time on the early foliage but soon left the station in which the study was made. Diptera were abundant during the estival period, while many of the animals which spend their entire life cycle in the forest were in early stages of reproduction and were not taken in any great numbers. Hymenoptera were very common in the collections of the entire summer, but Cicadellidae were not abundant until the hot, dry weather caused the maturation of nymphal forms in the late estival and early serotinal periods.

6. There was a marked increase of the total population in the upper strata during the autumn, with migrating species of leafhoppers again forming an important part of the collections. The low night minimum temperatures together with other physical and biotic factors may have been important in stimulating this prehibernation movement of the animals. The number of animals in the upper strata decreased after the first killing frost (October 24), with the exception of a few species, and hibernating species appeared in greater numbers in the ground collections. These migratory movements were essentially the same as those reported by Weese (1924).

7. An analysis of the meteorological observations showed a greater gradient of physical factors from the ground to the shrub stratum than from the shrub to the tree stratum. This would seem to indicate that animals in moving from the ground into upper strata would encounter definite differences of physical fac-

tors which might greatly influence them in their stratal distribution. An analysis of the stratal distribution of the animals collected, showed many species to be rather definitely limited to certain strata although biotic and other factors were probably important, as well as physical ones, in determining their distribution. Some species, as *Dictyna* sp. among the spiders, showed little evidence of stratification.

8. The invertebrate animals of the deciduous forest seem to be rather regularly distributed as to strata with seasonal changes of strata being evident for the premigratory period of the early spring and the prehibernation period of the autumn. At times there were diurnal movements, particularly of some groups, as has been observed during short periods of study by other workers.

9. This appears to mean that the animals of the forest are on the whole stratified; those of the leaf mat on the ground being largely confined to this stratum, those on the herbs to the herb stratum, those on the shrubs to the shrub stratum, and those in the trees to the tree stratum. In other words, while there was some diurnal movement from strata to strata on the part of some species, on the whole this was negligible. The study, therefore, substantiates the work of most previous workers who treated their material as though there were a definite stratification of invertebrates.

APPENDIX

LIST OF ANIMALS COLLECTED

A. In Leaf Stratum

Thysanura:
  Machilidae:
    Machilis sp. (Oct. 9).
  Japygidae
    Japyx sp. (Oct. 30).
Collembola:
  Aphoruridae:
    Neanura muscorum Temp. (Nov. 13).
  Entomobryidae:
    Entomobrya purpurascens Pck. (Oct. 6, 14, 16, 20, 30; Nov. 6, 13, 17, 20; Dec. 4).
    Isotoma sp. (Nov. 13).
    Orchesella ainsliei Fols. (Jan. 9; Oct. 16, 20, 23).
    Tomocerus flavescens Tull. var. *americanus* Schott. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 9, 16, 30; Feb. 13; Mr. 12; May 28; June 4, 11, 16, 25; July 2, 9, 16, 23, 30; Aug. 6, 13; Oct. 2, 6, 9, 14, 16, 20, 25, 27, 30; Nov. 3, 6, 10, 13, 17, 20, 27; Dec. 4, 11, 16, 25).
  Miscellaneous:
    Ptenothrix sp. (Nov. 21; Dec. 12; June 18; Oct. 2, 9, 20, 30; Nov. 6, 10, 13, 17, 20).
Orthoptera:
  Locustidae:
    Melanoplus sp. (Aug. 20-nymph).
  Tettigoniidae:
    Ceuthophilus sp. nymph (Apr. 2, 16; May 7; Oct. 2).
  Gryllidae:
    Gryllus assimilis Fabr. nymph (Jan. 23).
    Gryllus sp. nymph (June 4, 11, 25).
    Hapithus agitator Uhler (June 18-nymph, 25; July 16).
  Blattidae:
    Parcoblatta sp. (Nov. 17, 20; Dec. 4).

Corrodentia:
  Psocidae:
    Ectopsocus californicus Banks (Nov. 21, 28; Dec. 12; Jan. 30-nymph; Oct. 20; Nov. 10).
Homoptera:
  Cicadellidae:
    Erythroneura sp. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 12, 19, 26; Apr. 2, 9, 16; Oct. 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 17, 20, 27; Dec. 4, 18, 25).
    Erythroneura harpax Beam. (Nov. 28; Dec. 5, 12; Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27).
    Erythroneura vulnerata Fh. (Nov. 21; Jan. 2; Mr. 5; Oct. 14; Nov. 20; Dec. 18).
    Erythroneura osborni DeL. (Oct. 23; Nov. 10).
    Erythroneura obliqua Say (Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 12, 19, 26; Apr. 2, 9; Oct. 14, 16, 23, 27; Nov. 3, 6, 10, 13, 17, 20, 27; Dec. 4, 11, 18, 25).
    Erythroneura basalis Say (Dec. 5, 12; Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 19, 26; Apr. 2, 9; Oct. 27; Nov. 13).
    Erythroneura tricincta Fh. (Nov. 28; Dec. 12, 19; Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 12, 19, 26; Apr. 2, 9; Oct. 14, 20, 23, 27, 30; Nov. 3, 10, 27; Dec. 4).
    Erythroneura vitis Harr. (Dec. 12, 19; Jan. 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 19, 26; Apr. 2, 9).
    Erythroneura comes Say (Dec. 5, 12; Jan. 16; Oct. 9, 14, 16, 27; Nov. 6, 27).
    Erythroneura noevus (Gill.) (Nov. 28; Dec. 5, 12, 19; Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 12, 19, 26; Apr. 2, 9; Oct. 23; Nov. 10).
    Empoasca sp. (Dec. 5, 12, 19; Jan. 2, 9, 16; Feb. 6, 20, 27; Mr. 12; Oct. 23; Nov. 6, 10, 17; Dec. 4, 25).
    Hymetta distincta Fairb. (Nov. 28; Dec. 5, 12, 19; Jan. 2, 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 5, 12, 19, 26; Apr. 2, 16; Oct. 9, 14, 20, 23, 27; Nov. 3, 10, 13, 17, 20; Dec. 4, 18).
    Scaphoideus productus Osb. (Oct. 14).
    Scaphoideus sp. (June 11).
    Platymetopius sp. nymph (May 28).
    Dikraneura cruentata Gill. (Oct. 9, 30; Nov. 10).
    Agallia sp. (Nov. 10).
    Graphocephala versuta (Say) (Dec. 5; Jan. 9; Feb. 20; Dec. 4).
  Miscellaneous:
    Catonia sp. nymph (June 11).
  Aphididae:
    Callipterini (Nov. 6, 10).
    Myzocallis n. sp. ? (Oct. 14, 27).
    Tritogenaphis ambrosiae (Thos.) (Nov. 10).
Hemiptera:
  Pentatomidae:
    Euschistus tristigmus Say (Nov. 21, 28; Dec. 19; Jan. 16; Feb. 20; Mr. 12, 26; Apr. 2).
  Coreidae:
    Acanthocephala declivis (Say) ? (Oct. 9; Nov. 10).
    Leptoglossus sp. (Apr. 9).
  Neididae:
    Jalysus spinosus Say (Dec. 5; Jan. 9).
  Lygaeidae:
    Cryphula parallelogramma Stal. nymph (Apr. 30; May 7, 14; July 2, 16, 30; Aug. 6).
  Reduviidae:
    Zelus exsanguis Stal. nymph (Mr. 26).
  Nabidae:
    Nabis sordida Reut. (June 4).
  Miridae:
    Lygus pratensis L. (Jan. 9, 16; June 4).
    Lygus sp. nymph (May 21).
    Fulvius sp. nymph (June 4, 11, 18-adult; July 2, 23).
  Corimelaenidae:
    Allocoris agrella McAtee (June 4, 11, 18; July 30).

Coleoptera:
  Carabidae:
    Harpalus sp. (prob. compar Lee.) (July 16).
    Harpalus sp. (July 16).
    Anillus sp. (June 4, 25; July 2, 9; Oct. 6; Nov. 3).
    Apenes sinuata Say (Oct. 14).
  Silphidae:
    Adelops mitchellensis Hatch (Nov. 3).
  Staphylinidae:
    Atheta sp. (June 4; Oct. 9).
  Lampyridae:
    Photuris sp. (Nov. 10; Dec. 4).
  Cantharidae:
    Cantharis sp. (June 25).
  Anthicidae:
    Tomoderus constrictus (Say) (July 23).
  Coccinellidae:
    Chilocorus bivulneratus Muls. (Nov. 10).
  Lathriidae:
    Melanophthalma distinguenda Com. (May 28).
  Tenebrionidae:
    Hoplocephala bicornis Fab. (July 23).
  Scarabaeidae:
    Phyllophaga fusca (Froelich) (May 14).
    Diplotaxis sp. (Apr. 30; Aug. 13).
    Aphodius sp. (Nov. 21).
  Chrysomelidae:
    Diabrotica duodecimpuncta Oliv. (Nov. 13).
    Diabrotica vittata (Fab.) Auct. (Apr. 16; Nov. 13).
    Longitarsus solidaginis Horn. ? (May 21).
    Xanthonia sp. (June 4, 25; July 23).
    Haltica sp. (Apr. 23).
  Cerambycidae:
    Cyrtinus pygmaeus Hald. (June 4).
  Cucujidae:
    Telephanus biguttatus (Say) (May 28).
  Mylabridae:
    Acanthoscelides musculus (Say) (Oct. 20).
  Curculionidae:
    Apion porcatum Boh. (Oct. 30).
Diptera:
  Tipulidae:
    Tipula sp. (Jan. 9).
  Mycetophilidae:
    Sciara petaini (Pettey) (Nov. 28; May 7; June 4, 25).
    Sciara sp. (Mr. 26; Oct. 9, 14).
    Mycetophila punctata Meig. (Jan. 30; Feb. 20; Apr. 2, 9, 16; Nov. 17).
  Psychodidae:
    Psychoda interdicta Dyar (Oct. 27).
  Ceratopogonidae:
    Culicoides sp. (June 4).
  Cecidomyiidae:
    Cecidomyia sp. (Apr. 2).
    Diplosis sp. (Oct. 16, 27; Nov. 6).
    Hormomyia sp. (July 30; Aug. 6).
  Empididae:
    Rhamphomyia sp. (Oct. 27).
  Phoridae:
    Megaselia scalaris Lw. (Nov. 27).
    Megaselia sp. (Oct. 14, 27).
  Drosophilidae:
    Drosophila sp. (Nov. 6).
  Agromyzidae:
    Phytomyza sp. (May 28).
Lepidoptera:
  Noctuidae:
    Parastichtis bicolorago (Gn.) (Nov. 17).
  Gracilariidae:
    Lithocolletis robiniella Clemens (Nov. 17).
Hymenoptera:
  Braconidae:
    Gyrocampa sp. (June 4).
    Synaldis sp. (July 30).
  Ichneumonidae:
    Camarotops sp. (Oct. 9).
    Gelis sp. (Oct. 20).

  Pteromalidae:
    Pteromalus sp. (Oct. 6).
  Serphoidea:
    Aphanogmus sp. (July 2).
    Piestopleura n. sp. (Oct. 6).
  Formicidae:
    Monomorium minimum (Buckley) (Oct. 6, 30).
    Myrmecina graminicola americana Emory (June 11, 25; July 2; Aug. 13, 20).
    Aphaenogaster texana var. (May 7, 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 6, 27; Nov. 6).
    Prenolepis imparis (Say) (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 16, 23; Feb. 6, 13, 20, 27; Mr. 5, 19, 26; Apr. 2, 16, 23, 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 2; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 27; Dec. 4, 25).
    Leptothorax curvispinosus Mayr. (Apr. 2, 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 16, 30; Aug. 6, 13, 20; Oct. 2, 6, 16, 30).
    Camponotus sp. Dec. 5; June 11; July 9, 23; Oct. 9, 30).
    Ponera coarctata pennsylvanica (Buckley) (June 18).
  Bethylidae:
    Aphelopus sp. (June 11).
    Holepyris sp. (Oct. 6, 27).
Chelonethida:
  Chthonidae:
    Chthonius pennsylvanicus Hag. (July 2; Oct. 6; Nov. 10).
Phalangiida:
  Phalangiidae:
    Liobunum formosum Wood (May 14; June 4, 11).
  Nemastomatidae:
    Nemastoma kepharti Crosby (Mr. 5; June 25; July 2).
Araneae:
  Dictynidae:
    Dictyna foliacea Hentz (Mr. 19; May 7; June 4; Nov. 27; Dec. 4).
    Dictyna sp. (prob. foliacea Hentz) (Nov. 21; Jan. 9, 23; May 7; June 18; Oct. 2, 16; Nov. 27; Dec. 25).
  Theridiidae:
    Euryopis sp. (Dec. 19; July 9; Oct. 6).
    Theridion sp. (Nov. 21; Feb. 6; Mr. 19; Apr. 16; Oct. 9).
    Crustulina sp. (July 2; Oct. 9, 20).
  Linyphiidae:
    Microneta sp. (Nov. 28; June 25; July 2; Oct. 2, 16, 27, 30; Nov. 10).
    Erigone sp. (Jan. 30).
    Ceraticelus alticeps (Fox) (Oct. 2).
    Ceratinopsis interpres (Cambr.) (Feb. 6).
    Lephthyphantes sp. (Mr. 5; Apr. 2, 9; May 7; June 11; July 16; Oct. 2, 6, 20).
    Linyphia communis Hentz (Apr. 9; Dec. 4).
  Argiopidae:
    Araenus sp. (July 9).
    Mangora placida Hentz (Jan. 16).
  Thomisidae:
    Tmarus caudatus Hentz (July 23; Oct. 6).
    Tmarus sp. (Jan. 2).
    Misumessus asperatus Hentz (Nov. 21; Mr. 19).
    Xysticus sp. (Dec. 19; Jan. 16; Feb. 27; July 23; Oct. 2, 6, 14, 16, 30; Nov. 6, 10, 13).
    Synema parvula Hentz (Feb. 20; Nov. 13).
    Philodromus exilis Banks (June 4).
  Ctenidae:
    Ctenus sp. (Oct. 27).
  Clubionidae:
    Anyphaena celer (Hentz) (Dec. 19; Jan. 2, 30; Feb. 20, 27; Mr. 5; Apr. 9; Oct. 2, 6, 27, 30; Nov. 3, 6, 17, 20, 27; Dec. 4, 18, 25).
    Anyphaenella saltabunda (Hentz) (Nov. 21; Feb. 20; Dec. 4).
    Castianeira cingulata C. Koch. (June 25; Oct. 9).

Castianeira sp. ? (Dec. 12; Apr. 2; Oct. 6).
Phurolithus sp. (Oct. 2, 6, 9, 14, 20; Nov. 6, 13, 20, 27; Dec. 4).

Lycosidae:
Pardosa milvina Hentz (Nov. 21; Dec. 5, 12, 19; Jan. 2, 16, 23; Feb. 20, 27; Mr. 5, 19, 26; Apr. 2, 16, 23, 30; May 7, 14, 21; June 4, 11, 25; July 9, 23, 30; Aug. 6, 13, 20; Oct. 2, 9, 20, 27, 30; Nov. 6, 10, 13, 27; Dec. 18, 25).
Pardosa sp. (Nov. 21; Jan. 2, 23; Mr. 19; Apr. 9; Oct. 20).
Lycosa sp. (Mr. 19; May 28; July 16, 23, 30; Aug. 6; Dec. 4, 25).
Trochosa litoralis Hentz (May 7, 21).
Trochosa sp. (Apr. 2).
Pirata sp. (May 28; Oct. 6; Nov. 6, 13, 17, 20, 27).

Attidae:
Dendryphantes octavus Hentz (Nov. 28; Apr. 2).
Dendryphantes nubilis Hentz (Mr. 19).
Dendryphantes canadensis Banks (June 11, 18; Oct. 6; Nov. 20).
Dendryphantes sp. (Dec. 5; Apr. 2, 9, 16).

Hahniidae:
Hahnia agilis Key. (Jan. 23, 30; July 9).
Hahnia sp. (Jan. 2; July 16).

Miscellaneous:
Cornicularia communis Emert. (Aug. 6; Nov. 13).
Grammonota sp. ? (July 2).

Acarina:
Erythraeidae:
Erythraeus sp. (Oct. 6, 20; Nov. 17, 20).

Parasitidae:
Parasitus sp. (July 16; Aug. 20; Oct. 6, 20; Nov. 13).

Ixodidae:
Dermacentor variabilis Say (Feb. 27; June 11, 25; July 16).
Dermacentor sp. immature (Dec. 12; Apr. 30; May 14, 21).

Bdellidae:
Bdella sp. (June 18; Oct. 6, 30; Nov. 17).

Trombidiidae:
Trombidium sp. (May 28; June 4, 11; Aug. 13; Oct. 2, 6; Nov. 27; Dec. 11).

Oribatidae:
Oribata minuta Banks (Oct. 6).

Miscellaneous:
Atomus sp. (Aug. 20; Oct. 20, 30).

Diplopoda:
Polyxenidae:
Polyxenus fasciculatus (Say) (July 9; Oct. 2, 9; Nov. 20).

Julidae:
Parajulus pennsylvanicus (Brandt) (Apr. 30; May 7, 21, 28; June 18, 25; Oct. 2, 9).

Polydesmidae:
Polydesmus sp. (July 2, 16, 23, 30; Aug. 20).

Polyzoniidae:
Polyzonium bivargatum (Wood) (Aug. 20).

Miscellaneous:
Cleidogonia caesioannulata (Wood) (June 25; July 2, 16; Oct. 6, 14).
Nannaria sp. (Oct. 9; Nov. 13, 17).
Spirostrephon lactarium (Say) (May 7; Oct. 9).

Chilopoda:
Scolopendridae:
Theatops posticus (Say) (Aug. 20).
Otocryptops sexspinosus (Say) (Aug. 13; Nov. 27).

Miscellaneous:
Tidabius sp. (July 2, 9, 16; Oct. 6, 30; Nov. 3, 13; Dec. 4).
Arenophilus bipuncticeps (Wood) (July 2).

Pulmonata:
Helicidae:
Stenotrema stenotrema (Pfr.) (Oct. 20, 27; Nov. 20; Dec. 4).
Polygyra thyroidus (Say) (Apr. 2, 30; May 21, 28; June 11, 18, 25; July 2; Oct. 2, 20; Nov. 3, 13).

Haplotrematidae:
Haplotrema concavum (Say) (Oct. 6; Nov. 10).

Zonitidae:
Zonitoides demissus (Binney) (June 4, 11, 18, 25; July 2, 9, 16; Aug. 6, 13, 20; Oct. 6, 9, 16, 20).
Paravitrea capsella (Gld.) (Oct. 23; Nov. 17).
Retinella indentata (Say) (July 9, 16).

B. In Herb Stratum

Collembola:
Entomobryidae:
Entomobrya purpurascens Pck. (Oct. 20, 23).
Tomocerus flavescens Tull. var. *americanus* Schott. (Nov. 28; Dec. 12, 19; Jan. 16; Apr. 30; July 9; Nov. 27).
Orchesella ainsliei Fols. (Jan. 16).

Miscellaneous:
Ptenothrix sp. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 16, 23; Feb. 13; Mr. 19, 26; Apr. 23; May 7, 14, 21; June 4, 18, 25; July 2, 9, 16, 23; Oct. 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 27; Dec. 4, 18, 25).

Orthoptera:
Locustidae:
Melanoplus sp. nymph (May 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 16).

Tettigoniidae:
Microcentrum sp. nymph (June 18).

Gryllidae:
Hapithus agitator Uhler nymph (June 4, 11; July 9, 16, 23).
Oecanthus sp. nymph (June 4, 18, 25; July 16; Aug. 13-adult).

Corrodentia:
Psocidae:
Ectopsocus californicus Banks (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 16; Feb. 13; July 2, 16; Aug. 6, 13).
Psocus montivagus Chapman (Aug. 20; Oct. 14).
Caecilius aurantiacus (Hagen) (Oct. 23; Nov. 3).

Neuroptera:
Hemerobiidae:
Micromus posticus (Walker) (Jan. 9; Feb. 6, 13; Nov. 27).

Homoptera:
Cicadellidae:
Erythroneura sp. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 16; Feb. 6, 27; Mr. 19, 26; Apr. 2, 9, 16, 23, 30; May 7, 14, 21, 28; June 11, 18, 25; July 2, 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 10).
Erythroneura harpax Beamer (Dec. 12).
Erythroneura vulnerata Fh. (Apr. 30; May 14; Oct. 6, 16, 20, 23, 27, 30; Nov. 3, 27; Dec. 25).
Erythroneura osborni DeL. (Oct. 9, 14, 23).
Erythroneura obliqua Say (Jan. 30; May 14; Apr. 2; Oct. 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 13, 27).
Erythroneura basalis Say (Apr. 9; May 14; Oct. 14, 16).
Erythroneura tricincta Fh. (Dec. 12; Apr. 9; May 7; Aug. 20; Oct. 9, 14, 16, 20, 27, 30; Nov. 3).
Erythroneura vitis Harr. (Dec. 19; Apr. 2, 9, 16; Aug. 6; Oct. 14, 23).
Erythroneura comes Say (Nov. 21; Dec. 12; Aug. 6, 20; Oct. 2, 9, 14, 16, 27).
Erythroneura noevus (Gill.) (Feb. 27; Apr. 9; July 16; Oct. 16, 20).
Empoasca sp. (Nov. 21; Jan. 16; Feb. 6; Apr. 9; Aug. 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 17).
Hymetta distincta Fairb. (Apr. 16; July 16, 30; Aug. 20; Oct. 9, 14, 16, 20, 23, 27, 30; Nov. 27).
Jassus olitorius Say (July 16, 23; Aug. 13, 20; Oct. 2, 20).
Jassus sp. nymph (May 7, 14, 21, 28; June 4, 11, 25; July 2, 9, 30; Aug. 13; Oct. 2).

Scaphoideus productus Osb. nymph (May 21; July 16, 23, 30; Aug. 6, 13, 20; Oct. 6, 16, 20; Nov. 10, 13).

Balclutha punctata Thunb. (Dec. 19; Apr. 9; Nov. 6).

Dikraneura cruentata Gill. (July 16; Oct. 9, 14, 16, 20, 23, 27, 30; Nov. 6).

Platymetopius sp. (June 4, 18, 25; July 9).

Platymetopius sp. nymph (July 9, 16, 23, 30; Aug. 13).

Gypona sp. nymph (May 21, 28; June 4, 18; July 23; Aug. 6).

Graphocephala versuta (Say) (Dec. 19; Jan. 2, 23; Feb. 20, 27; Mr. 5, 19, 23; Apr. 2; May 28; Oct. 6, 9, 14, 16, 23, 27; Nov. 6, 10, 13, 27; Dec. 25).

Cicadella occatoria Say (July 9).

Miscellaneous:

Dolla geometrica Sign. (July 16).

Aphelonema sp. (June 25; Aug. 20-nymph).

Thionia bullata (Say) (June 25; July 9; Aug. 20).

Catonia sp. nymph (June 11, 18, 25; July 2, 9).

Fulgoridae:

Ormenis pruinosa Say (July 2, 16, 23, 30).

Ormenis sp. (June 18, 25; July 2-nymph).

Acanalonia sp. (July 2).

Psyllidae:

Psylla carpinicola Crawf. (Oct. 16, 30; Nov. 3).

Pachysylla celtidis Riley (Nov. 6).

Trioza diospyri Ashm. (May 28; June 11; July 30).

Aphididae:

Callipterini (Nov. 21; May 7; June 18-immat.; July 30; Aug. 20; Oct. 2, 6, 14, 20, 23, 27, 30; Nov. 3, 6, 10).

Macrosiphum pisi (Kalt.) (May 28; July 23; Aug. 6; Oct. 14).

Myzocallis n. sp. ? (Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 6, 13, 17).

Tritogenaphis ambrosiae (Thos.) (Nov. 21; Oct. 14, 20, 23, 27; Nov. 3, 6).

Longistigma coryae (Harris) (Oct. 30).

Monellia caryae (Mon.) (July 30).

Aleyrodidae (Oct. 9, 14, 16, 20, 27, 30; Nov. 3, 6, 10, 13).

Hemiptera:

Pentatomidae:

Euschistus tristigmus Say (Nov. 21, 28; Dec. 19; Jan. 2; Feb. 20; July 9; Aug. 6; Oct. 27).

Thyanta custator (Fabr.) (Dec. 19; Jan. 9, 16; Apr. 2; Oct. 27, 30).

Brochymena quadripustulata (F.) (Nov. 20).

Coreidae:

Acanthocephala terminalis (Dall.) nymph (June 25; July 16).

Acanthocephala declivis (Say) ? (Nov. 3).

Neididae:

Jalysus spinosus Say (Nov. 21, 28; Feb. 6; Apr. 2, 16; June 25; Aug. 6, 20; Oct. 2, 9; Nov. 3).

Aradidae:

Aradus sp. (July 16).

Lygaeidae:

Cryphula parallelogramma Stal. (May 7, 28).

Tingidae:

Corythucha sp. (May 7).

Phymatidae:

Phymata pennsylvanica Handl. (Nov. 10).

Reduviidae:

Sinea diadema (Fabr.) (Jan. 16).

Sinea spinipes (H. S.) (Oct. 14).

Sinea sp. (Nov. 21; June 25; July 2-nymph, 23-nymph; Aug. 13-nymph, 20-nymph; Oct. 2).

Zelus exsanguis Stal. (Feb. 13; May 7; Oct. 20-nymph; Nov. 6-nymph).

Nabidae:

Nabis roseipennis Reut. (Dec. 19; Apr. 23-nymph; Oct. 6; Nov. 27; Dec. 25).

Nabis ferus Reut. (Jan. 2).

Nabis annulatus Reut. (July 16; Aug. 13; Oct. 20).

Nabis annulatus Reut. nymph (July 16, 23, 30; Aug. 6, 13).

Nabis sordida Reut. nymph (Oct. 20).

Anthocoridae:

Orius insidious (Say) (Nov. 13).

Miridae:

Lygus pratensis L. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 9, 16, 23, 30; Feb. 6; Nov. 3, 13, 27; Dec. 4, 18, 25).

Lygus quercalbae Knight (May 28; June 18).

Lygus sp. nymph (May 7, 21; June 4).

Hyaliodes vitripennis (Say) (June 11, 18, 25; July 9; Oct. 9).

Hyaliodes vitripennis (Say) nymph (June 11, 25; July 2, 9, 16; Aug. 13, 20).

Reuteria irrorata (Say) (Aug. 20).

Plagiognathus sp. (May 28; June 4, 25).

Phytocoris pallidicornis Reut. (May 28; July 16-nymph).

Orthotylus sp. (May 28; June 4).

Corimelaenidae:

Allocoris agrella McAtee (Apr. 30; May 7, 14, 21, 28; June 18, 25; July 9, 16; Aug. 6, 13, 20; Oct. 9).

Coleoptera:

Carabidae:

Lebia ornata Say (June 4).

Staphylinidae:

Atheta sp. (Dec. 19).

Silphidae:

Adelops mitchellensis Hatch (Nov. 10).

Adelops sp. (Nov. 3).

Phalaeridae:

Acylomus sp. (Jan. 2, 9).

Histeridae:

Saprinus sp. (June 18).

Cantharidae:

Cantharis lincola F. (May 28; June 4, 18).

Cantharis sp. (May 14, 21).

Buprestidae:

Agrilus sp. (Oct. 23).

Elateridae:

Ludius signaticollis Melsh. (May 21, 28; June 18; July 9).

Cleridae:

Enocleris quadrisignatus Say (June 4).

Coccinellidae:

Delphastus sp. (July 30; Oct. 6).

Chilocorus bivulneratus Muls. (Jan. 30).

Scymnus sp. (July 9; Aug. 13).

Psyllobora vingtemaculata Say (Apr. 16; Aug. 6).

Lathriidae:

Melanophthalma distinguenda Com. (Nov. 21; Dec. 5, 12, 19; Jan. 2, 16; Feb. 13; Apr. 16, 23, 30; May 7, 14, 21, 28; June 11; July 9, 16, 23; Oct. 14, 20, 23, 27, 30; Nov. 3, 6, 27; Dec. 18, 25).

Orthoperidae:

Orthoperus glaber Lec. (July 16).

Ptinidae:

Ptinus bimaculatus Melsh. (May 7).

Malachiidae:

Pseudebaeus sp. (June 11).

Attalus sp. (July 9).

Anobiidae:

Protheca hispida Lec. (June 18).

Chrysomelidae:

Chlamys gibbosa Auct. (Oct. 30).

Xanthonia decimnotata (Say) (June 18; July 2).

Xanthonia sp. (May 28; June 4, 11, 18, 25; July 2, 16, 23; Aug. 6; Oct. 6, 9).

Rhabdopterus praetexta (Say) (July 2).

Diabrotica vittata (Fab.) Auct. (Apr. 16; May 21; June 4; Oct. 9, 16).

Longitarsus solidaginis Horn? (Nov. 21, 28; Jan. 2, 16; Apr. 9, 16, 23, 30; May 7, 14, 21, 28; June 4, 11, 18; July 2, 9; Aug. 6, 13, 20; Oct. 2, 6, 14, 16, 20, 23; Nov. 3, 6, 13; Dec. 18).

Baliosus ruber (Weber) (June 25; July 2, 16, 23, 30; Aug. 6).
Anoplitis inaequalis ? (Weber) (Aug. 13; Oct. 16, 20).
Cerambycidae:
Cyrtinus pygmaeus Hald. (May 21; July 2).
Hipposis lemniscata F. (July 9).
Mylabridae:
Gibbibruchus mimus Say (July 9; Nov. 6).
Melandryidae:
Symphora rugosa Hald. (May 14; June 18; Aug. 6).
Mordellidae:
Mordellistena sp. (May 28; June 11, 18, 25; July 9, 16, 23, 30; Aug. 6, 13; Nov. 3).
Oedemeridae:
Microtonus sericans Lec. (May 14).
Anthicidae:
Anthicus sp. (July 2).
Notoxus bicolor Say (Oct. 2).
Byturidae:
Byturus unicolor Say (July 2, 16).
Euglenidae:
Zonantes fasciatus (Melsh.) (June 25; Aug. 20; Oct. 27).
Curculionidae:
Apion turbulentum Smith (May 14, 21, 28; June 18; July 2, 16, 30; Aug. 6, 13, 20; Oct. 14).
Zaglyptus sulcatus Lec. (Apr. 30).
Eugnamptus sp. (June 18).
Diptera:
Tipulidae:
Tipula duplex Wlk. (July 16).
Tipula abdominalis Say (May 7; June 11).
Tipula sp. (Feb. 27; Apr. 2).
Helobia sp. ? (Mr. 19, 26).
Dicranoptycha winnemani Alex. (May 28; June 18; July 2, 9).
Dicranoptycha sp. (July 16, 23).
Cladura flavoferruginea O. S. (Oct. 20, 27; Nov. 3).
Mycetophilidae:
Sciara petaini (Pettey) (Nov. 21; Apr. 30; May 7, 14, 21, 28; June 4, 18, 25; July 2, 9; Aug. 13, 20; Oct. 30).
Sciara sp. (Nov. 28; Dec. 19; Apr. 23, 30; May 7, 14, 28; June 4, 11, 18, 25; July 2, 16, 23; Oct. 14, 16, 20, 23, 27; Nov. 6).
Mycetophila punctata Meig. (Mr. 26; Apr. 23; May 14).
Mycetophila sp. (Apr. 16; May 21, 28; June 4, 11; Oct. 20).
Coelosia sp. (May 28).
Platyura sp. (May 28; June 4, 11, 25.)
Macrocera immaculata Johns. (June 18).
Boletina sp. (Oct. 30; Nov. 13; Dec. 4).
Psychodidae:
Psychoda interdicta Dyar (Nov. 6, 13).
Culicidae:
Aedes mitchellae (Dyar) (June 4, 11).
Aedes trivittatus (Coq.) (Aug. 6, 13).
Chironomidae:
Chironomus sp. (Apr. 30; May 14).
Pseudochironomus sp. (Apr. 23, 30; May 14, 21; July 2).
Cricotopus sp. (Apr. 23, 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 9, 30).
Chasmatonotus sp. (Apr. 30).
Ceratopogonidae:
Atrichopogon fusculus (Coq.) (May 21; June 18).
Atrichopogon sp. (June 4; July 9; Oct. 30).
Culicoides melleus (Coq.) (June 25).
Monohelea sp. (June 18).
Dasyhelea sp. (July 23; Oct. 16).
Stilobezzia sp.? (June 11; Aug. 13).
Serromyia crassifemorata Mall. (May 21).
Forcipomyia sp. (July 23).
Cecidomyiidae:
Diplosis sp. (Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 6).

Hormomyia sp. (June 18; July 23, 30; Aug. 20; Oct. 2).
Asilidae:
Leptogaster sp. (June 18, 25; July 23, 30; Oct. 2).
Stratiomyiidae:
Stratiomyia sp. (May 21).
Rhagionidae:
Rhagio vertebratus Say (May 28).
Therevidae:
Thereva sp. (May 14).
Empididae:
Rhamphomyia sp. (Oct. 16).
Hybos sp. (June 25; Oct. 2, 23).
Drapetis sp. (May 7).
Chelipoda sp. (May 14, 28).
Dolichopodidae:
Dolichopus sp. (May 14).
Leucostola cingulata Lw. (May 21, 28; June 4).
Leucostola sp. (May 21; Oct. 2, 6).
Porphyrops sp. ? (May 21).
Argyra flavipes V. D. (May 28; June 4, 18, 25).
Argyra sp. (June 11).
Gymnopternus sp. (May 28; June 4; Aug. 13; Oct. 27).
Pelastoneurus sp. (May 21; June 11; Aug. 20).
Neurigona sp. (June 11).
Diaphorus sp. (Aug. 6).
Phoridae:
Megaselia scalaris Lw. (July 9, 16, 23, 30; Aug. 6, 13, 20).
Megaselia sp. (May 21, 28; June 4, 11, 18, 25; July 2, 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2).
Platypezidae:
Platypeza sp. (July 30).
Pipunculidae:
Pipunculus sp. (May 28; July 16; Aug. 20).
Chalarus spurius Fallen (July 16).
Syrphidae:
Syrphus americanus Wied. (Apr. 9).
Sarcophagidae:
Sarcophaga sp. (Aug. 13; Oct. 23).
Calliphoridae:
Lucilia sp. (Nov. 28; Dec. 12).
Muscidae:
Phaonia sp. (Aug. 13; Oct. 14, 16).
Mydaea sp. (June 11, 25; July 2, 9).
Scatophagidae:
Scatophaga stercoraria (L.) (Mr. 19; Apr. 9).
Sciomyzidae:
Leria sp. (Dec. 19).
Sapromyzidae:
Sapromyza bispina Lw. (May 28; June 4, 25; Aug. 6, 13).
Sapromyza umbrosa Lw. (June 18).
Sapromyza sp. (May 28; June 4, 11, 18; July 9, 23, 30; Aug. 6; Oct. 20).
Homoneura sp. (Aug. 6; Oct. 2).
Minettia quadrilineata Lw. (May 28; June 4, 18, 25; July 9, 23, 30; Aug. 6, 13, 20).
Minettia magna Coq. (June 18).
Minettia sp. (May 14, 21; June 16; Aug. 13).
Borboridae:
Leptocera sp. (July 9).
Chloropidae:
Chloropisca glabra (Mg.) (Aug. 6, 20; Oct. 30; Nov. 6).
Oscinella sp. (May 28; June 11, 25; July 23, 30).
Drosophilidae:
Drosophila sp. (Oct. 6; Nov. 27).
Leucophenga sp. (June 11, 18, 25; July 16, 23, 30; Aug. 6, 13, 20).
Agromyzidae:
Neophyllomyza sp. (May 7, 14; June 4, 11, 18; July 30).
Phytomyza sp. (Apr. 16, 30; May 7, 21, 28; June 11, 18, 25; July 2, 9, 16, 23; Aug. 6).
Trichoceridae:
Trichocera sp. (Oct. 23; Nov. 27; Dec. 4).

Lepidoptera:
  Noctuidae:
    Parastichtis bicolorago (Gn.) (Dec. 4).
  Pyralidae:
    Pyrausta sp. (May 7; June 4, 11, 18, 25; July 9; Aug. 13).
    Perispastus caeculalis Zell. (July 23).
  Gelechiidae:
    Aristotelia sp. (June 18, 25; July 2, 9, 16, 23).
  Gracilariidae:
    Lithocolletis robiniella Clements (Apr. 23).
Hymenoptera:
  Braconidae:
    Opius sp. (May 7, 21; June 4, 11; July 9, 16; Aug. 6, 13; Oct. 14, 16).
    Apanteles sp. (Apr. 2, 16; June 4; Aug. 13, 20; Oct. 2, 20).
    Microgaster facetosa Weed (May 14; June 4; July 30).
    Microbracon variabilis (Prov.) (July 23, 30).
    Meteorus n. sp. (Oct. 14; Nov. 10).
    Dorycetes sp. (Aug. 6).
    Schizoprymnus texanus Cress. (June 25).
    Phanerotoma sp. (June 11, 18, 25).
    Aspilota sp. (Dec. 19; Apr. 30; June 4; July 2; Oct. 27).
    Microtonus n. sp. (July 23).
    Gyrocampa sp. (Apr. 16, 23, 30; May 7, 21, 28; July 23, 30).
    Spathius sp. (June 4).
    Orthostigma sp. (July 23).
    Idiasta sp. (May 14, 21, 28; June 18, 25).
    Heterospilus sp. (May 14, 21; July 2; Aug. 6, 13).
    Synaldis sp. (June 4, 18; July 9, 23; Oct. 2, 6).
    Dacnusa sp. (June 11; July 9; Aug. 6).
    Ecphylus sp. (July 30).
    Macrocentrus harrisi Degant (Oct. 6).
    Aridelus nigrithorax Nues. (July 9).
  Ichneumonidae:
    Glypta sp. (Apr. 16; May 21; July 30).
    Aperileptus sp. (May 21; June 4, 11, 25; Aug. 6; Oct. 14, 20).
    Phygadeuon sp. (June 4; July 2; Aug. 13).
    Enicospilus purgatus (Say) (June 11).
    Amblyteles album (Cress.) (Aug. 13; Oct. 6, 13).
    Thymaris americanus Cush. (June 25).
    Casinaria infesta (Cress.) June 25; July 23; Aug. 6).
    Phaeogenes sp. (Oct. 16; Nov. 13).
    Gelis sp. (Aug. 6, 20; Oct. 14).
    Phaedroctonus sp. (Aug. 6).
    Thysiotorus sp. (Oct. 14).
  Cynipidae:
    Odonteucoila sp. (June 18; Aug. 13).
  Figitidae:
    Charips sp. (Oct. 23).
    Eucoila sp. (July 23, 30; Aug. 6).
  Tetrastichidae:
    Tetrastichus sp. (July 9; Aug. 6; Oct. 16).
    Chrysocharoideus sp. (July 9; Aug. 6; Oct. 16).
    Hyperteles sp. (June 11).
  Entedontidae:
    Entedon sp. (Apr. 30).
    Omphale bicincta Ashm. (Oct. 6).
    Chrysocharis sp. (Apr. 30; May 7, 28; July 9, 16; Aug. 13; Nov. 3).
  Eulophidae:
    Pnigalio metacomet (Crawf.) (June 18; Aug. 20).
    Pnigalio proximus (Ashm.) (Apr. 30; May 14; June 11, 25).
    Sympiesis sp. (July 30).
  Elachertidae:
    Euplectrus n. sp. (Aug. 20; Oct. 20, 27).
  Pteromalidae:
    Pteromalus sp. (May 7; June 25; July 23).
    Zatropis sp. (July 9; Aug. 13, 20).
  Aphelinidae:
    Prospaltella sp. (June 25; July 2; Oct. 30).

  Encyrtidae:
    Cheiloneurus n. sp. (July 9).
    Anagyrus sp. (July 30; Oct. 27).
    Microterys cinctecornis Ashm. (Oct. 14, 23).
  Eupelmidae:
    Anastatus mirabilis (Walsh) (June 11; July 30).
  Chalcidoidea:
    Eupelmella n. sp. (June 4).
  Calliceratidae:
    Calliceras sp. (May 21; June 11; July 9, 23; Aug. 20).
    Aphanogmus sp. (July 2, 23; Aug. 6).
  Platygastridae:
    Platygaster sp. (Aug. 13; Oct. 6, 30).
    Leptacis americana (Ashm.) (June 18; July 16; Aug. 20; Oct. 6, 20, 27).
    Amblyaspis n. sp. (July 2; Oct. 16).
  Scelionidae:
    Telenomus n. sp. (July 16, 23, 30).
    Trissolcus euschisti Ashm. (Apr. 2).
  Diapriidae:
    Trichopria sp. (July 30).
    Xenotoma sp. (July 16; Aug. 13; Oct. 16).
    Spilomicrus sp. ? (May 14; June 18; Aug. 20).
    Belyta sp. (May 7, 28).
  Formicidae:
    Monomorium minimum (Buckley) (May 21; June 4, 18; July 16; Oct. 6, 16, 20, 30).
    Tapinoma sessile (Say) (May 21).
    Brachymyrmex sp. (July 9).
    Myrmecina graminicola americana Emory (Oct. 2, 6).
    Aphaenogaster texana var. (June 25; July 2; Aug. 6).
    Prenolepis imparis (Say) (Nov. 21, 28; Jan. 16; Feb. 27; Mr. 5; Apr. 2, 9, 16, 23, 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 16, 23; Aug. 6, 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 27).
    Leptothorax curvispinosus Mayr. (Mr. 12, 26; Apr. 2, 9, 16, 23, 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 6, 16, 30).
    Camponotus caryae rasilus Whlr. (May 28; June 4; July 9; Oct. 6).
    Camponotus sp. (Apr. 16; July 16; Oct. 6).
  Sphecidae:
    Spilomena sp. (May 28; July 23).
  Bethylidae:
    Gonatopus sp. (Aug. 6).
    Chelogynus sp. (May 21; June 4).
    Holepyris sp. (July 9).
    Rhabdepyris sp. ? (Oct. 20).
  Scoliidae:
    Tiphia sp. (July 16).
  Psammocharidae:
    Planiceps sp. (June 4).
  Halictidae:
    Halictus sp. (Aug. 6).
Phalangiida:
  Phalangiidae:
    Liobunum formosum (Wood) (Apr. 16, 30; May 7, 21; July 16).
Araneae:
  Uloboridae:
    Uloborus americanus Walck. (Jan. 16).
    Uloborus sp. (Oct. 6, 23).
    Hyptiotes cavatus Hentz (Jan. 2).
  Dictynidae:
    Dictyna foliacea Hentz (Mr. 19; Apr. 9, 23, 30; May 14, 28; June 4; Oct. 2).
    Dictyna sp. (prob. foliacea Hentz) (Apr. 16, 23, 30; May 7, 21; June 11; July 30; Oct. 2, 9, 14, 16, 20, 23, 27, 30; Nov. 3).
  Theridiidae:
    Euryopis sp. (Dec. 5, 12; Jan. 2, 9; Feb. 6, 27; Apr. 2; July 9, 30; Aug. 6; Oct. 27, 30; Nov. 6; Dec. 25).

Theridion frondeum Hentz (June 18).
Theridion sp. (Apr. 23; July 9, 23; Oct. 14, 16, 20, 27; Nov. 3, 6, 27; Dec. 25).
Theridula sphaerula (Hentz) (Dec. 18).
Argyrodes sp. (Aug. 20).
Linyphiidae:
Ceraticelus alticeps (Fox) ? (Aug. 6; Oct. 27).
Ceratinopsis interpres (Cambr.) (Dec. 12; Jan. 2, 9, 16; Feb. 6, 13, 20, 27; Apr. 2, 16, 30; May 7, 14, 28; June 4, 11, 25; July 30; Aug. 20; Oct. 2, 6, 9, 14, 16, 20, 30; Nov. 3, 6, 10, 13, 17, 27; Dec. 4, 18, 25).
Ceratinopsis laticeps Emer. (Oct. 27).
Lephthyphantes sp. (Nov. 28; Apr. 9; June 25; Oct. 14; Nov. 13).
Linyphia communis Hentz. (Dec. 5; Jan. 2, 30; Feb. 13, 27; Mr. 19, 26; Apr. 2; July 16; Aug. 6; Oct. 2, 23, 27, 30; Nov. 6; Dec. 4).
Argiopidae:
Tetragnatha sp. (Nov. 27).
Leucauge hortorum Hentz (Dec. 5; Jan. 2, 16, 30; Feb. 6, 20, 27; Mr. 19, 26; Apr. 2, 16; May 7, 14, 21; June 11, 25; July 9; Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 13, 17, 27; Dec. 4, 18, 25).
Singa nigriceps Keys. (May 21).
Singa truncata Banks (May 7).
Wixia sp. (Nov. 28; Jan. 30; Feb. 27; Oct. 23; Nov. 27; Dec. 25).
Araneus sp. (Feb. 6, 27).
Mangora placida Hentz (Nov. 28; Dec. 19; Feb. 6, 20; Mr. 26; Apr. 9; May 28; July 23, 30; Aug. 13; Oct. 6, 9, 14, 20; Dec. 4).
Mangora maculata Keys. (May 28; July 9, 16, 23, 30; Aug. 13; Nov. 3).
Mangora sp. (Apr. 9; June 4, 18; July 2; Aug. 6, 9).
Mimetidae:
Mimetus sp. (June 11; Oct. 14).
Thomisidae:
Tmarus caudatus Hentz (Nov. 28; Dec. 5, 12, 19; Jan. 2, 9, 16, 23; Feb. 6, 13, 20, 27; Mr. 19, 26; Apr. 2, 9, 16; May 14; July 16, 30; Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 17, 27; Dec. 4, 18, 25).
Misumessus asperatus Hentz (Nov. 21, 28; Dec. 12; Jan. 16, 23, 30; Feb. 13; Apr. 9, 23; May 14; June 25; July 2; Oct. 23; Nov. 3, 6, 13, 27; Dec. 25).
Xysticus triguttatus Key (Apr. 16).
Xysticus sp. (Mr. 19; July 16).
Synema parvula Hentz (Nov. 28; Dec. 5, 12, 19; Jan. 2, 9, 16; Feb. 6, 13, 20, 27; Apr. 2, 9, 16, 30; May 14, 21; July 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 16, 20, 27, 30; Nov. 3, 6, 10; Dec. 18).
Philodromus sp. (Nov. 27; Dec. 18).
Tibellus oblongus (Walck.) (Oct. 30).
Tibellus sp. (Dec. 12).
Clubionidae:
Anyphaena celer (Hentz) (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 16, 23, 30; Feb. 6, 13, 20; June 18, 25; July 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 17, 27; Dec. 4, 18, 25).
Anyphaenella saltabunda (Hentz) (July 9, 23; Aug. 20; Oct. 16).
Trachelas tranquilla Hentz ? (Feb. 13).
Pisauridae:
Dolomedes sp. (June 4; Oct. 20; Nov. 3, 6, 17; Dec. 18).
Lycosidae:
Lycosa sp. (Feb. 6).
Pardosa milvina Hentz (Aug. 6).
Pardosa sp. (Dec. 5).
Pirata piratica (Clerck) (Feb. 20).
Pirata sp. (Jan. 23, 30).
Oxyopidae:
Oxyopes sp. (Dec. 19; May 21; July 9).

Attidae:
Dendryphantes octavus Hentz (Jan. 30; Feb. 6, 27; Nov. 13, 20).
Dendryphantes sp. (Jan. 9; Feb. 20; Mr. 19; Apr. 2, 9, 30; Aug. 20; Oct. 20, 30; Nov. 6, 17).
Synemosyna formica Hentz (July 9; Oct. 20).
Maevia vittata (Hentz) (May 21; June 4; July 23; Oct. 6).
Thiodina sp. ? (Aug. 13; Oct. 2, 30).
Miscellaneous:
Grammonota sp. ? (July 9; Dec. 25).
Acarina:
Erythraeidae:
Erythraeus sp. (June 18; July 9, 23; Oct. 14).
Parasitidae:
Uropoda sp. (July 2).
Ixodidae:
Dermacentor variabilis Say (May 14, 21; June 18, 25; July 2, 9, 16).
Bdellidae:
Bdella sp. (June 18; July 9; Aug. 13).
Trombidiidae:
Trombidium sp. (May 21; June 4; Oct. 2).
Oribatidae:
Oribata minuta Banks (July 9).
Diplopoda:
Polyxenidae:
Polyxenus fasciculatus (Say) (July 9, 16, 23, 30; Aug. 6, 13, 20).
Miscellaneous:
Spirostrephon lactarium (Say) (July 9).
Pulmonata:
Helicidae:
Polygyra thyroidus (Say) (Jan. 23; Apr. 30; May 21, 28; June 25; July 2, 9, 23; Oct. 6, 30).
Zonitidae:
Zonitoides demissus (Binney) (June 4, 25; July 2; Oct. 23).
Retinella indentata (Say) (July 30).

C. In Shrub Stratum

Collembola:
Entomobryidae:
Tomocerus flavescens Tull. var. *americanus* Schott (Apr. 30; Nov. 27).
Miscellaneous:
Ptenothrix sp. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 2, 16, 23; Apr. 23; May 7, 14; June 18, 25; July 2, 16, 23; Aug. 13; Oct. 14, 16, 20, 23, 27; Nov. 6, 13, 17, 27; Dec. 4, 18, 25).
Orthoptera:
Phasmatidae:
Diapheromera femorata (Say) (Aug. 6-nymph).
Tettigoniidae:
Microcentrum sp. (July 9-nymph).
Gryllidae:
Hapithus agitator Uhler (June 4-nymph, 11-nymph, 18-nymph, 25; July 9, 16; Aug. 13).
Oecanthus sp. (June 11, 25; July 9-nymph; Aug. 13-nymph, 20).
Corrodentia:
Psocidae:
Ectopsocus californicus Banks (Nov. 28; Dec. 12, 19; Jan. 2, 9, 16, 23; Feb. 13; May 7; June 11; July 2, 16, 30; Aug. 6, 13, 20; Oct. 6, 16-immat., 20-immat.; Nov. 13-immat., 27).
Psocus montivagus Chapman (June 18, 25; Aug. 13-adults and nymphs, 20-nymph; Oct. 16).
Caecilius aurantiacus (Hagen) (Oct. 23, 27, 30).
Neuroptera:
Hemerobiidae:
Micromus posticus (Walker) (Dec. 5; Jan. 16; Oct. 6).
Chrysopidae:
Chrysopa lineaticornis Fitch (Aug. 6).
Coniopterygidae:
Coniopteryx vicini Hagen (June 4, 11).

Mecoptera:
  Bittacusidae:
    Bittacus apicalis Hagen (Oct. 6).
Homoptera:
  Cicadellidae:
    Erythroneura sp. (Nov. 21, 28; Dec. 5, 12, 19; Jan. 16, 23; Mr. 5, 19; Apr. 2, 9, 16, 23, 30; May 7, 14, 28; June 4, 11, 18, 25; July 2, 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 13, 27).
    Erythroneura harpax Beam. (Nov. 21; Dec. 5, 12).
    Erythroneura vulnerata Fh. (Feb. 20; Apr. 16, 30; July 23; Oct. 6, 20, 30; Nov. 10).
    Erythroneura osborni De L. (Oct. 2, 14, 27).
    Erythroneura obliqua Say (Jan. 30; Feb. 27; Apr. 2, 9, 16; Oct. 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 27).
    Erythroneura basalis Say (Apr. 9, 16, 23, 30; Oct. 14, 20).
    Erythroneura tricincta Fh. (Nov. 21; Dec. 12, 19; Mar. 19; Apr. 2, 9, 30; Aug. 6, 13; Oct. 6, 14, 16, 20, 23, 27, 30).
    Erythroneura vitis Harr. (Dec. 19; Jan. 16; Apr. 2, 9, 16; Oct. 14).
    Erythroneura comes Say (Nov. 21, 28; Dec. 12, 19; Aug. 20; Oct. 2, 6, 16, 27, 30).
    Erythroneura noevus (Gill.) (Dec. 12, 19; Apr. 2, 16; Oct. 9, 20, 23, 30).
    Empoasca sp. (Nov. 21; Dec. 12, 19; Jan. 16; Feb. 6; Mr. 19; Apr. 23; Aug. 6; Oct. 2, 6, 9, 14, 16, 20, 23; Nov. 3, 6; Dec. 4).
    Jassus olitorius Say (July 9, 23; Aug. 6; Oct. 16; Nov. 6).
    Jassus sp.-nymph (May 7, 14, 21, 28; June 4, 11, 18; July 2, 16, 23, 30; Aug. 13; Nov. 3).
    Hymetta distincta Fairb. (Nov. 21; Feb. 27; Apr. 16; Aug. 6, 20; Oct. 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3).
    Scaphoideus productus Osb. (May 28; June 4; Aug. 20; Oct. 6, 9; Nov. 10).
    Platymetopius sp.-nymph (July 9, 23, 30; Aug. 6).
    Gypona sp.-nymph (May 21, 28; June 25-adult; July 9, 16).
    Agallia novella Say (Aug. 6).
  Miscellaneous:
    Aphelonema sp.-nymph (July 9; Aug. 20).
    Thionia bullata (Say) (July 9, 16, 23; Aug. 6, 20-nymph).
    Catonia sp.-nymph (June 4, 11, 18, 25; July 9, 16).
  Fulgoridae:
    Ormenis pruinosa Say (July 2, 9, 16, 23, 30; Aug. 13, 20).
    Ormenis sp.-nymph (July 2, 9; Aug. 13, 20).
    Acanalonia sp. (June 25; July 9).
  Psyllidae:
    Trioza diospyri Ashm. (May 21, 28; June 18, 25; July 2, 23; Oct. 6).
    Psylla sp. (Nov. 27, 1937).
    Pachysylla celtidis Riley (Nov. 6; Dec. 11; 1937).
  Aphididae:
    Callipterini (Nov. 21; May 7; July 30; Aug. 6, 13, 20; Oct. 2, 6, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13, 17).
    Macrosiphum pisi (Kalt.) (Aug. 6).
    Myzocallis n. sp. (Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10, 13).
    Monellia caryae (Mon.) (July 30).
  Aleyrodidae:
    Aleyrodidae (Aug. 13; Oct. 2, 6, 9, 14, 20; Nov. 3).
Hemiptera:
  Pentatomidae:
    Euschistus tristigmus Say (Apr. 2; July 30; Oct. 20; Nov. 6).
    Euschistus sp. (Dec. 12).
    Brochymena quadripustulata (F.) (Aug. 20).
    Brochymena sp. (Apr. 9).
    Thyanta custator (Fab.) (Oct. 9).
    Chlorochroa uhleri Stal. (Oct. 23, 30).

Coreidae:
    Acanthocephala terminalis (Dall.)-nymph (July 2, 25).
Neididae:
    Jalysus spinosus Say (Apr. 16; Oct. 20).
Lygadidae:
    Cryphula parallelogramma-nymph (May 28; June 25; July 9).
    Nysius minutus Uhl. (Oct. 27).
Reduviidae:
    Sinea sp.-nymph (May 21; June 25).
    Zelus exsanguis Stal.-nymph (Oct. 14, 27; Nov. 3, 13).
Nabidae:
    Nabis roscipennis Reut. (July 23; Aug. 13-nymph; Oct. 6).
    Nabis annulatus Reut. (July 9, 16; Aug. 20).
    Nabis annulatus Reut.-nymph (July 16; Aug. 6).
    Nabis sordida Reut. (June 25).
Miridae:
    Lygus pratensis L. (Dec. 12, 19; Feb. 27; Nov. 13).
    Lygus quercalbae Knight (June 18; July 9).
    Lygus sp.-nymph (May 21).
    Hyaliodes vitripennis (Say) (Aug. 6, 13, 20).
    Hyaliodes vitripennis (Say)-nymph (June 4, 18, 25; July 2, 9, 16; Aug. 20).
    Reuteria irroraria (Say)-nymph (July 16).
    Plagiognathus sp. (June 4, 11, 18, 25).
    Orthotylus sp. ? (June 11).
Corimelaenidae:
    Allocoris agrella McAtee (Apr. 16; May 21).
Coleoptera:
  Carabidae:
    Lebia viridis (June 25).
  Staphylinidae:
    Oleocharinae (July 2, 9).
    Atheta sp. (May 14).
  Hydrophilidae:
    Cercyon nigriceps Marsh. (June 18).
  Phalacridae:
    Litochrus sp. ? (Apr. 30; May 14).
  Cantharidae:
    Cantharis sp. (May 7, 14; June 11, 18).
    Cantharis lineola F. (May 28).
  Cleridae:
    Enocleris sp. (July 2).
  Elateridae:
    Melanotus sp. (July 9).
  Coccinellidae:
    Delphastus sp. (Apr. 23, 30; May 14, 21, 28; Oct. 6, 9, 14, 16, 20, 30).
    Chilocorus bivulneratus Muls (Apr. 9).
    Cycloneda munda Say (June 25).
    Scymnus sp. (Aug. 6; Oct. 27).
    Psyllobora vingtemaculata Say (Apr. 2, 9, 23, 30; July 23; Oct. 2).
  Lathriidae:
    Melanophthalma distinguenda Com. (Nov. 28; Dec. 19; Apr. 2, 23, 30; May 7, 21; June 11; Oct. 6, 14, 27, 30; Nov. 3).
    Lathridius liratus Lec. (May 21; July 23).
  Orthoperidae:
    Orthoperus glaber Lec. (May 7).
  Anobiidae:
    Caenocara lateralis Lec. (May 14).
  Chrysomelidae:
    Xanthonia sp. (May 7, 14, 28; June 4, 11, 18, 25; July 9, 16, 23; Aug. 13).
    Diabrotica vittata Auct. (Apr. 16; May 14, 21; June 18; Oct. 2, 6, 9, 14, 30).
    Longitarsus solidaginis ? Horn (Feb. 13; Apr. 2, 23; May 14, 21; July 30; Aug. 6; Oct. 6, 30).
  Mylabridae:
    Gibbibruchus mimus (Say) (Apr. 23, 30; June 4; July 9).
    Acanthoscelides musculus (Say) (June 18).
  Melandryidae:
    Symphora sp. (May 21).

Mordellidae:
  Mordellistena sp. (July 9, 23, 30).
Oedemeridae:
  Microtonus sericans Lec. (May 14, 21; June 25).
  Microtonus sp. (May 7, 21).
Anthicidae:
  Notoxus bicolor Say (Oct. 6).
Curculionidae:
  Apion turbulentum Smith (Apr. 9; May 7, 14, 21, 28; June 4, 18; July 2, 9; Oct. 6, 14).
  Eugnamptus collaris F., var. (June 18; July 9, 30).
Euglenidae:
  Vanonus sp. (June 11).
  Zonantes fasciatus (Melsh.) (July 30).
Melasidae:
  Rhagomicrus bonvouloiri Horn (July 9, 16).
Phalacridae:
  Acylomus sp. (July 16).
Scolytidae:
  Corthylus punctatissimus Zinam. (June 11).
Diptera:
Tipulidae:
  Tipula sp. (Jan. 2; Apr. 30; June 11).
  Tipula abdominalis Say (May 28).
  Dicranoptycha winnemani Alex. (May 28; June 11, 18, 25; July 2, 9, 23).
  Cladura flavoferruginea O. S. (Oct. 27, 30; Nov. 13).
Mycetophilidae:
  Sciara petaini (Pettey) (Apr. 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 2, 9; Oct. 6).
  Sciara sp. (Apr. 30; May 7; June 11, 18; July 16, 23; Oct. 9, 14, 16, 20, 30; Nov. 10, 27).
  Mycetophila punctata Meig. (Jan. 23).
  Mycetophila sp. (Jan. 2, 23; May 28; June 4, 11).
  Cordyla neglecta Joh. ? (Nov. 3, 6).
  Boletina sp. (Dec. 4, 1937).
Psychodidae:
  Psychoda interdicta Dyar (Oct. 16, 20, 27).
Culicidae:
  Aedes mitchellae (Dyar) (June 4).
  Aedes trivittatus (Coq.) ? (June 4; July 2; Aug. 6).
Chironomidae:
  Chironomus sp. (Apr. 30; May 7, 21, 28; June 4; July 23; Oct. 27).
  Chasmatonotus sp. (Apr. 30; May 7).
  Pseudochironomus sp. (April 16, 23; May 14, 21, 28).
  Cricotopus sp. (Apr. 23, 30; May 14, 21, 28; June 4).
  Spaniotoma sp. (July 2, 9, 16).
Ceratopogonidae:
  Atrichopogon fusculus (Coq.) (June 4, 11, 18).
  Culicoides guttipennis (Coq.) (July 16; Oct. 14).
  Culicoides melleus (Coq.) (May 28; June 4; July 2).
  Dasyhelea sp. (July 2, 16, 23).
  Stilobezzia sp. (June 25).
  Serromyia crassifemorata Mall. (May 14).
Asilidae:
  Leptogaster sp. (June 18; July 23).
Ceeidomyiidae:
  Hormomyia sp. (June 18; July 23, 30; Oct. 6).
Rhagionidae:
  Rhagio vertebratus Say (May 28).
  Chrysopilus sp. (June 25).
Therevidae:
  Thereva sp. (May 14).
Empididae:
  Rhamphomyia sp. (Oct. 23, 27).
  Hybos sp. (June 18, 25).
  Drapetis sp. ? (May 14, 28; July 23).
  Chelipoda sp. (May 14).
  Hoplocyrtoma sp. (June 11).
  Syneches sp. (June 18).
  Oreothalia sp. ? (May 7).
Dolichopodidae:
  Leucostola cingulata Lw. (May 21, 28).
  Gymnopternus sp. (June 18).
  Pelastoneurus sp. (May 28).
  Argyra flavipes V. D. (June 4).

Phoridae:
  Megaselia scalaris Lw. (July 16, 23; Aug. 6, 13).
  Megaselia sp. (Apr. 9; June 18, 25; July 2, 9, 23, 30; Aug. 6, 13, 20; Oct. 20, 30).
Syrphidae:
  Syrphus sp. (May 28).
Sarcophagidae:
  Sarcophaga rapax Walk. (May 21; Aug. 20).
  Sarcophaga sp. (June 18; July 9, 16, 23; Aug. 6; Oct. 27).
Calliphoridae:
  Lucilia caeruleiviridis Macq. (June 18).
  Lucilia sp. (Dec. 12; July 2).
Muscidae:
  Phaonia sp. (July 16, 23).
Scatophagidae:
  Scatophaga stercoraria (L.) (Jan. 9; Feb. 20; Mr. 5, 19; Apr. 16, 23; Nov. 6).
Trypetidae:
  Straussia sp. (Nov. 10).
Psilidae:
  Chyliza notata Lw. (May 14).
Chloropidae:
  Chloropisca glabra (Mg.) (July 9, 16, 23).
  Oscinella sp. (May 28; June 4).
Drosophilidae:
  Drosophila sp. (Oct. 30).
  Leucophenga sp. (June 25; July 2, 9, 16, 23; Aug. 13; Oct. 27).
Agromyzidae:
  Phytomyza sp. (Mr. 19; Apr. 16, 23, 30; May 7; June 4, 11, 18, 25; July 16; Oct. 20).
  Neophyllomyza sp. (May 7, 14; June 4, 11).
Sapromyzidae:
  Sapromyza bispina Lw. (July 23; Aug. 6, 13).
  Sapromyza sp. (May 21, 28; June 11, 18; July 16, 23; Aug. 20).
  Minettia quadrilineata Lw. (Apr. 23; May 28; June 4, 25; July 16; Aug. 6, 13, 20).
  Minettia magna (Coq.) (Apr. 23; May 28; July 16).
  Minettia sp. (Apr. 2, 30; May 14; June 4).
  Homoneura sp. (July 16).
Trichoceridae:
  Trichocera sp. (Nov. 13; Dec. 4).
Mieropezidae:
  Nerius sp. (June 18).
Lepidoptera:
Noctiidae:
  Parastichtis bicolorago (Gn) (Nov. 13).
Pyralidae:
  Pyrausta sp. (May 14; June 4, 18).
Geleehiidae:
  Aristotelia sp. (June 18, 25).
Gracilariidae:
  Lethocolletis robiniella Clemens (Apr. 16; July 9).
Hymenoptera:
Braconidae:
  Opius sp. (May 14, 21, 28; June 11, 25; Oct. 6).
  Apanteles sp. (Apr. 2; June 18, 25).
  Apanteles conanchetorum Vier. (July 9, 30; Aug. 6; Oct. 16).
  Microbracon variabilis (Prov.) (Nov. 3).
  Dorycetes sp. (July 9; Oct. 14, 30).
  Schizoprymnus texanus Cress. (May 21, 28).
  Phanerotoma sp. (June 11, 18, 25; Oct. 6).
  Rogas nolophanae Ashm. (Oct. 9, 20, 30).
  Aspilota sp. (Dec. 19; May 14, 21; June 4).
  Microtonus n. sp. (May 28; Aug. 20).
  Gyrocampa sp. (Apr. 23, 30; May 7, 14, 21; June 4, 25; July 2, 9, 30; Aug. 13).
  Orthostigma sp. (July 9; Oct. 6).
  Idiasta sp. (May 28; June 4; July 2).
  Heterospilus sp. (May 7, 21, 28; July 2).
  Synaldis sp. (June 4; July 9).
  Aridelus fisheri Vier. (June 11).
Ichneumonidae:
  Aperileptus sp. (May 28; June 18).
  Thymaris americanus Cush. (June 4; Aug. 13).

Neotheronia winnemanae Vier. (July 2, 9).
Amblyteles album (Cress.) (July 16).
Glypta sp. (Aug. 13).
Gelis sp. (Oct. 9, 30; Nov. 6).
Camarotops sp. (Oct. 30).

Figitidae:
Eucoila sp. (July 23, 30).

Mymaridae:
Anagrus epos Gir. (Oct. 16, 20).
Gonatocerus novifasciatus Gir. (Oct. 20, 27).

Tetrastichidae:
Tetrastichus sp. (Aug. 6, 13; Oct. 30).
Hyperteles sp. (July 2).

Entedontidae:
Omphale sp. (Nov. 3).
Chrysocharis sp. (May 7, 21).

Eulophidae:
Pnigalio proximus (Ashm.) (Apr. 23, 30; May 7, 14; June 25).

Pteromalidae:
Pterosema sp. (July 30).

Aphelinidae:
Prospaltella sp. (Oct. 14).

Encyrtidae:
Anagyrus sp. (Aug. 13, 20; Oct. 20).

Eupelmidae:
Eupelmella n. sp. (May 6).
Chrysocharoideus sp. (Aug. 6).

Platygastridae:
Platygaster sp. (Oct. 20, 23, 27).
Leptacis americana (Ashm.) (July 9, 16, 23; Aug. 13; Oct. 6, 14, 20, 30).
Amblyaspis n. sp. near *petiolata* Ashm. (July 2; Aug. 6, 13; Nov. 3).

Scelionidae:
Trissolcus euschisti Ashm. (Mar. 26; Apr. 2; June 4; July 2, 9; Aug. 6).
Trissolcus podisti Ashm. (Apr. 16).
Telenomus n. sp. (July 9, 16; Oct. 20, 27, 30; Nov. 13).

Diapriidae:
Trichopria appar. new (Aug. 6).
Belyta sp. (May 7, 28; June 18).

Serphoidea:
Calliceras sp. (May 14).
Phaenoserphus abruptus (Say) (June 18).
Aphanogmus sp. (June 18; July 2; Oct. 6).
Xenotoma sp. (July 9; Oct. 30).

Formicidae:
Aphaenogaster texana var. (June 4).
Monomorium minimum (Buckley) (May 14, 21; June 4, 11; Oct. 6, 27, 30).
Myrmecina graminicola americana Emory (Oct. 6).
Prenolepis imparis (Say) (Nov. 21, 28; Dec. 5, 12; Jan. 2, 16, 23; Feb. 6, 27; Mr. 5, 26; Apr. 2, 9, 16, 23, 30; May 7, 14, 28; June 4, 11, 18, 25; July 2, 9, 16; Aug. 13; Oct. 2, 6, 9, 14, 20, 27, 30; Nov. 6, 13, 27).
Leptothorax curvispinosus Mayr. (Mr. 19; Apr. 2, 9, 16, 23, 30; May 7, 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 16, 23, 30; Aug. 6, 13; Oct. 6, 30).
Camponotus sp. (May 7; June 25; Oct. 9, 14).
Camponotus caryae rasilus Whlr. (June 4; July 9).

Sphecidae:
Stigmus sp. (May 14; June 18; July 9; Aug. 6).
Psen angulatus Malloch (Aug. 6).

Bethylidae:
Chelogynus sp. (June 18, 25).
Aphelopus comesi (Fenton) (June 18, 25; Oct. 20).
Gonatopus sp. (July 30; Oct. 30).

Scoliidae:
Tiphia sp. (Aug. 13).

Halictidae:
Halictus stultus Cr. (Aug. 6).

Phalangiida:
Phalangiidae:
Liobunum formosum Wood (May 7, 21).

Araneae:
Uloboridae:
Uloborus sp. (Nov. 6).

Dictynidae:
Dictyna foliacea Hentz (Feb. 20; May 7, 14, 28; June 4, 18; Oct. 2).
Dictyna sp. (prob. *foliacea* Hentz) (Jan. 23; Feb. 6; Apr. 16, 30; May 7; July 30; Aug. 13; Oct. 6, 9, 14, 16, 23, 30).

Theridiidae:
Theridion frondeum Hentz (June 18; July 23).
Theridion sp. (prob. *spiralis* Emer.) (Feb. 6; Apr. 16; May 14; June 4, 11).
Theridion sp. (July 9, 23; Oct. 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 6, 10).
Theridula sphaerula Hentz (Oct. 16, 23, 30).
Euryopis sp. (Jan. 9).

Linyphiidae:
Ceratinopsis interpres (Cambr.) (Apr. 30; May 7, 14; June 11; July 9; Aug. 6; Oct. 2, 9, 14, 16; Dec. 4).
Microneta sp. (Nov. 28).
Lephthyphantes sp. (Oct. 14, 20, 27).
Linyphia communis Hentz (Dec. 5; Feb. 20, 27; Apr. 2, 30; Oct. 9, 14; Nov. 27; Dec. 18).

Argiopidae:
Tetragnatha sp. (Nov. 27).
Leucauge hortorum Hentz (Dec. 5, 19; Jan. 16, 30; Mr. 5, 26; Apr. 2; May 7; July 16; Aug. 13; Oct. 9, 14, 16, 20, 23, 27, 30; Nov. 6, 10, 13, 17, 27; Dec. 4, 18, 25).
Araneus sp. (Feb. 13).
Acacesia foliata (Hentz) (July 23).
Mangora placida Hentz (Dec. 5; Feb. 6, 20; Mr. 26; Apr. 9; May 28; June 18; Oct. 9; Nov. 3, 17, 27; Dec. 25).

Thomisidae:
Misumessus asperatus Hentz (Nov. 21; Feb. 27; Mr. 26; May 14; June 11; Oct. 23).
Tmarus caudatus Hentz (Dec. 5, 19; Jan. 9, 16, 23, 30; Feb. 6, 13, 20, 27; Mr. 19, 26; Apr. 2, 9, 16, 23; June 25; July 9, 16, 23, 30; Aug. 6, 13, 20; Oct. 2, 9, 16, 20, 27, 30; Nov. 3, 10, 27; Dec. 4, 18, 25).
Coriarachne versicolor Keys. (Feb. 6).
Xysticus sp. (Mr. 5; Apr. 2; Aug. 6).
Synema parvula Hentz (Apr. 9, 16, 23, 30; May 7, 14, 28; June 4; July 9; Aug. 20; Oct. 6, 20; Nov. 13).

Clubionidae:
Anyphaena celer (Hentz) (Jan. 23; June 11, 18, 25; July 2, 9, 16, 30; Aug. 6, 13; Oct. 6, 9, 14, 20, 23, 27, 30; Nov. 3, 6, 10, 13; Dec. 4, 25).
Anyphaenella saltabunda (Hentz) (July 9, 16, 23).
Castianeira sp. (Oct. 14).

Lycosidae:
Pardosa sp. (Oct. 30).

Attidae:
Dendryphantes octavus Hentz (Nov. 21; Oct. 20, 23, 27, 30).
Dendryphantes nubilis Hentz (Feb. 13; Mr. 19; Apr. 2, 16; May 14; Oct. 14, 27, 30).
Dendryphantes sp. (Dec. 12, 19; Jan. 16; Mr. 12, 26; Apr. 2, 9, 16, 23; May 28; Aug. 6; Oct. 9, 27; Nov. 6).
Maevia vittata (Hentz) (June 18).
Thiodina sp. ? (July 16).
Synemosyna formica Hentz (May 21; June 4; Oct. 16, 23; Nov. 17).

Miscellaneous:
Cornicularia communis Emer. (May 28).

Acarina:
Erythraeidae:
Erythraeus sp. (July 16; Oct. 14).
Parasitidae:
Uropoda sp. (Dec. 19).

Ixodidae:
　Dermacentor variabilis Say (May 7; June 11; July
　　9, 23).
Trombidiidae:
　Trombidium sp. (May 7, 14, 21; June 4).
Diplopoda:
　Polyxenidae:
　　Polyxenus fasciculatus (Say) (June 18; July 2, 16,
　　　23).
Pulmonata:
　Helicidae:
　　Polygyra thyroidus (Say) (Apr. 30).

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Collembola:
　Miscellaneous:
　　Ptenothrix sp. (Jan. 23; Mr. 5; May 21; June 18;
　　　July 23, 30; Oct. 20, 23, 27; Nov. 6, 10, 13, 27;
　　　Dec. 4, 18, 25).
Orthoptera:
　Tettigoniidae:
　　Microcentrum sp. (June 18-nymph; July 16).
　Gryllidae:
　　Hapithus agitator Uhler (June 4, 11, 18-nymph, 25;
　　　July 2, 9, 23; Aug. 20).
　　Oecanthus sp. (June 11, 18-nymph, 25; July 2-nymph,
　　　9-nymph, 23; Aug. 6-nymph).
　Blattidae:
　　Parcoblatta sp. (Nov. 20).
Corrodentia:
　Psocidae:
　　Ectopsocus californicus Banks (Dec. 12; June 18,
　　　25; July 9, 16; Aug. 6, 13; Oct. 2, 6-immat., 14,
　　　20).
　　Psocus montivagus Chapman (May 28; June 4, 11,
　　　18; July 30; Oct. 30).
Neuroptera:
　Chrysopidae:
　　Chrysopa lineaticornis Fitch (Aug. 13, 20).
Homoptera:
　Cicadellidae:
　　Erythroneura sp. (Nov. 28; Dec. 12, 19; Jan. 16,
　　　23; Feb. 6; Apr. 2, 9, 16, 23, 30; May 7, 14, 21,
　　　28; June 4, 11, 18, 25; July 2, 9, 16, 23, 30;
　　　Aug. 6, 13, 20; Oct. 2, 6, 9, 14, 20, 23, 27, 30;
　　　Nov. 3, 6).
　　Erythroneura harpax Beamer (Apr. 16, 23, 30; July
　　　23).
　　Erythroneura vulnerata Fh. (Nov. 28; Feb. 6; Apr.
　　　16, 23, 30; May 7, 14, 28; July 23; Aug. 6, 13;
　　　Oct. 6, 9, 14, 16, 20, 23, 27, 30; Nov. 6).
　　Erythroneura osborni DeL. (Oct. 2, 9, 14, 16, 20).
　　Erythroneura obliqua Say (Apr. 2, 16, 23, 30; May
　　　28; Aug. 13; Oct. 6, 9, 14, 16, 20, 27, 30; Nov. 3).
　　Erythroneura basalis Say (Apr. 9, 16, 23, 30; May
　　　7; Aug. 13, 20; Oct. 9, 14; Nov. 6).
　　Erythroneura tricincta Fh. (Jan. 30; Mr. 26; Apr.
　　　9, 16, 23, 30; May 7, 14, 28; July 30; Aug. 20;
　　　Oct. 9, 14, 16, 20, 30).
　　Erythroneura vitis Harr. (Jan. 23; Mr. 19; Apr. 9;
　　　May 7; Aug. 6, 13, 20; Oct. 9, 20).
　　Erythroneura comes Say (July 9, 16, 30; Aug. 6,
　　　13, 20; Oct. 2, 9, 14, 16, 20).
　　Erythroneura noevus (Gill.) (Apr. 9, 16; Aug. 20;
　　　Oct. 6, 16, 20, 27).
　　Empoasca sp. (Apr. 16; Oct. 9, 14, 16, 20, 23; Nov.
　　　6, 13, 27; Dec. 25).
　　Jassus olitorius Say (Aug. 6; Oct. 20, 27; Nov. 13).
　　Jassus sp. nymph (May 7, 14, 21, 28; June 4, 11;
　　　July 9, 16, 23).
　　Hymetta distincta Fairb. (Apr. 23, 30; May 7; July
　　　9, 30; Aug. 20; Oct. 2, 6, 14, 16, 20, 23, 30).
　　Scaphoideus productus Osb. (May 14, 21; June 4,
　　　25; July 9; Aug. 6, 13, 20; Nov. 13).
　　Scaphoideus sp. nymph (May 7).
　　Platymetopius sp. nymph (June 25; July 16, 23).
　　Gypona sp. nymph (June 4, 25—also adult; Aug.
　　　13).

Oncometopia undata (Fab.) (Oct. 27).
　Graphocephala versuta (Say) (Mr. 19; June 4; Oct.
　　14, 16, 20, 30; Nov. 6, 13).
Miscellaneous:
　Aphelonema sp. ? (May 28; June 4, 11; Aug. 20-
　　nymph).
　Thionia bullata (Say) (July 16, 23, 30; Aug. 6, 13,
　　20; Oct. 16, 20).
　Catonia sp. nymph (June 4, 11, 18; July 9).
Fulgoridae:
　Ormenis pruinosa Say (July 2, 9, 16, 30; Aug. 6,
　　13, 20).
　Ormenis sp. nymph (June 18, 25).
　Acanalonia sp. nymph (June 11).
Psyllidae:
　Trioza diospyri Ashm. (May 28; June 4, 18; July
　　30; Aug. 13).
　Psylla sp. (Nov. 3).
Aphididae:
　Callipterini (May 7, 14, 21, 28; July 16, 23, 30;
　　Aug. 6, 13, 20; Oct. 2, 6, 14, 16, 20, 23, 27, 30;
　　Nov. 3, 6, 10, 13).
　Macrosiphum pisi (Kalt.) (May 28; July 23, 30;
　　Aug. 6).
　Myzocallis n. sp. ? (Oct. 2, 6, 9, 14, 16, 20, 23, 37,
　　30; Nov. 3, 6, 10, 13).
　Tritogenaphis ambrosiae Thos. (Oct. 20, 27).
Aleyrodidae (July 9; Aug. 13; Oct. 6, 20, 23).
Hemiptera:
　Pentatomidae:
　　Euschistus tristigmus Say (July 9).
　　Brochymena quadripustulata (F.) (Nov. 10).
　　Brochymena arborea Say (Oct. 9).
　　Acrosternum hilaris (Say) (July 23, 30).
　Coreidae:
　　Acanthocephala declivis (Say) ? (Oct. 6).
　Lygaeidae:
　　Cryphula parallelogramma Stal. (June 4).
　　Cryphula parallelogramma Stal. nymph (June 4, 25;
　　　July 9).
　Reduviidae:
　　Sinea sp. (July 23).
　　Zelus exsanguis Stal. nymph (Oct. 16, 27).
　Nabidae:
　　Nabis annulatus Reut. nymph (Oct. 2).
　Miridae:
　　Lygus quercalbae Knight (June 11).
　　Lygus sp. nymph (May 21).
　　Plagiognathus sp. nymph (May 28; June 4).
　　Hyaliodes vitripennis (Say) (July 2, 9, 16, 23, 30;
　　　Aug. 6, 13, 20).
　　Hyaliodes vitripennis (Say) nymph (June 4, 11, 18,
　　　25; July 2, 23; Aug. 13).
　　Diaphnidia capitata Van D. ? (June 4; July 23, 30).
　　Phytocoris pallidicornis Reut. (June 4).
　　Orthotylus sp. ? (June 4, 18).
　　Reuteria irrorata (Say) (July 2, 9).
Coleoptera:
　Staphylinidae:
　　Atheta sp. (May 14).
　Phalacridae:
　　Litochrus sp. (Aug. 6).
　Cantharidae:
　　Cantharis sp. (May 14, 21; June 4).
　　Malthinus occipitalis Lec. (May 28).
　Cleridae:
　　Enocleris sp. larva (July 30).
　Melasidae:
　　Dirhagus triangularis Say (June 25).
　　Rhagomicrus bonvouloiri Horn (Aug. 13).
　Coccinellidae:
　　Delphastus sp. (May 14; Aug. 13; Oct. 6, 9, 16).
　　Chilocorus bivulneratus Muls. (Nov. 13).
　Lathriidae:
　　Melanophthalma distinguenda Com. (May 7, 14;
　　　June 4; Oct. 6, 16, 30).
　Orthoperidae:
　　Orthoperus glaber Lec. (May 7).

Malachiidae:
  Pseudebaeus sp. (May 28; June 4, 18).
Chrysomelidae:
  Longitarsus solidaginis Horn (Oct. 6).
  Diabrotica vittata (Fab.) Auct. (Apr. 23, 30; May 7).
  Haltica sp. (Apr. 23).
  Orthaltica copalina (F.) (June 18).
  Altica sp. (Oct. 14).
  Xanthonia sp. (May 28; June 4, 11, 18; July 23; Oct. 6).
  Baliosus ruber (Weber) (June 4).
Cerambycidae:
  Cyrtinus pygmaeus (Hald.) (May 21).
  Dorcaschema alternatum Say (June 18).
Mylabridae:
  Gibbibruchus mimus (Say) (Apr. 30).
Melandryidae:
  Symphora sp. (May 14; June 18; Oct. 20).
  Symphora rugosa (Hald. (May 28; June 4; July 9, 16, 23).
Mordellidae:
  Mordellistena sp. (May 28; June 18; July 2, 9, 16, 23; Aug. 13).
Oedemeridae:
  Microtonus sericans Lec. (May 21; June 4, 11; July 2).
Endomychidae:
  Endomychus biguttatus Say (Nov. 13).
Euglenidae:
  Zonantes fasciatus (Melsh.) (July 16, 23).
Curculionidae:
  Eugnamptus collaris Say (June 18).
  Eugnamptus sp. (June 18).
Diptera:
Tipulidae:
  Tipula sp. (June 4).
  Dicranoptycha winnemani Alex. (May 28; June 4).
  Nephrotoma ferruginea (F.) (Oct. 14).
Mycetophilidae:
  Sciara petaini (Pettey) (May 7, 14; June 4; July 2, 9, 30; Aug. 6; Oct. 6).
  Sciara sp. (Apr. 30; May 7, 28; June 4, 18, 25; Oct. 14, 16; Nov. 6).
Psychodidae:
  Psychoda interdicta Dyar (Nov. 13).
Culicidae:
  Aedes trivittatus (Coq.) (Oct. 16).
Chironomidae:
  Pseudochironomus sp. (Apr. 23, 30; May 14, 28).
  Chironomus sp. (Apr. 30; May 14; June 4, 11; July 2, 9, 30).
  Cricotopus sp. (Apr. 23; May 21, 28; June 4, 18; July 2, 30; Aug. 20).
Ceratopogonidae:
  Stilobezzia sp. (July 16).
  Dasyhelea sp. (July 2, 16, 23, 30; Aug. 6, 13, 20).
  Atrichopogon fusculus (Coq.) (June 11; Nov. 6).
  Culicoides melleus (Coq.) (May 21, 28; June 4, 11, 18, 25; July 2).
  Culicoides guttipennis (Coq.) (Aug. 6, 13).
Cecidomyiidae:
  Hormomyia sp. (July 23, 30; Aug. 13; Oct. 6).
Empididae:
  Chelipoda sp. (May 28; June 4, 18).
  Oreothalia sp. ? (May 21, 28; Oct. 30).
  Hoplocyrotoma sp. (Apr. 23).
Dolichopodidae:
  Gymnopternus sp. (May 28; June 4).
  Leucostola cingulata Lw. (May 21).
Phoridae:
  Megaselia scalaris Lw. (July 23, 30).
  Megaselia sp. (Feb. 27; June 4, 18; Oct. 30).
Muscidae:
  Phaonia sp. (July 23).
Scatophagidae:
  Scatophaga stercoraria (L.) (Dec. 5).

Psilidae:
  Chyliza sp. (Nov. 10).
Chloropidae:
  Pseudogaurax anchora (Lw.) (May 28; July 30; Aug. 20).
  Oscinella sp. (July 9, 23).
  Chloropisca glabra (Mg.) (July 16; Nov. 6).
  Chloropisca sp. (Aug. 13).
Drosophilidae:
  Drosophila sp. (Oct. 14; Nov. 3, 6).
  Leucophenga sp. (July 2, 9, 16, 23; Aug. 20; Oct. 27).
Agromyzidae:
  Phytomyza sp. (Apr. 16; May 21; June 4, 11).
  Neophyllomyza sp. (July 23).
Sapromyzidae:
  Sapromyza bispina Lw. (July 30).
  Sapromyza sp. (May 14; July 30).
  Homoneura sp. (June 25; July 16, 23, 30; Aug. 6, 20; Oct. 6).
  Minettia quadrilineata Lw. (May 28; June 4; July 23, 30; Aug. 6, 13, 20).
  Minettia magna Coq. (Apr. 16, 30; May 28; June 18; July 9, 16, 23, 30; Aug. 6, 20).
  Minettia sp. (Apr. 2, 9, 23, 30; May 21, 28; June 4).
Lonchaeidae:
  Lonchaea sp. (Apr. 23; May 28; June 11; July 16).
Lepidoptera:
Pyralidae:
  Pyrausta sp. (June 25).
Gelechiidae:
  Aristotelia sp. (June 18; July 23).
Gracilariidae:
  Lithocolletis robiniella Clemens (Dec. 12; Jan. 30; Feb. 6, 27; Mr. 26; June 18).
Hymenoptera:
Braconidae:
  Opius sp. (May 14, 28).
  Apanteles conanchetorum Vier. (July 9).
  Apanteles sp. (July 30).
  Dorycetes sp. (July 23).
  Phanerotoma sp. (June 25; July 2).
  Microtonus sp. (June 11; Oct. 2).
  Aspilota sp. (May 28).
  Gyrocampa sp. (May 7).
  Spathius sp. (May 28; June 4, 11, 25; Aug. 6, 13, 20).
  Idiasta sp. (May 14).
  Heterospilus sp. (May 7, 14; June 18; July 2, 23, 30; Oct. 2).
  Heterospilus beameri Roh. (May 7, 14; July 30).
  Synaldis sp. (July 4).
  Idhiaulax agrili (Ashm.) (May 14; July 16).
  Ecphylus sp. (May 28; June 18; July 23).
  Mirax lithocolletidis Ashm. (May 28).
  Mirax sp. (Aug. 13).
Ichneumonidae:
  Thymaris americanus Cush. (June 11).
Cynipidae:
  Odonteucoila sp. (June 4).
  Prosaspicera sp. (Oct. 9).
Mymaridae:
  Anagrus epos Gir. (Oct. 14, 20).
  Polynema n. sp. (June 4).
Eulophidae:
  Pnigalio proximus (Ashm.) (May 7).
  Pnigolio metacomet (Crawf.) (May 7; June 25; July 30).
  Pnigalio sp. (Aug. 6).
  Sympiesis sp. near marylandica Gir. (Oct. 27).
  Comedo anomocerus Cwfd. (Aug. 6).
Entedontidae:
  Chrysocharis sp. (May 14, 28; June 4; Oct. 20).
Pteromalidae:
  Pterosema sp. ? (May 7).
Encyrtidae:
  Microterys cincticornis Ashm. (Oct. 14, 23; Nov. 13).

Eupelmidae:
　Anastatus mirabilis (Walsh.) (June 4; July 9; Oct. 6).
Platygastridae:
　Amblyaspis n. sp. near petiolata Ashm. (June 25; Aug. 13).
　Leptacis americana (Ashm.) (July 30; Aug. 6, 13).
　Leptacis sp. (Aug. 13; Oct. 23, 30).
　Platygaster sp. (Aug. 6; Oct. 6, 14; Nov. 3).
Scelionidae:
　Trissolcus podisti Ashm. (Apr. 16).
　Trissolcus euschisti Ashm. (Apr. 2; June 11; July 23).
　Trissolcus sp. (July 2).
　Telenomus n. sp. (May 28; June 4; July 2, 9, 16, 23; Aug. 6, 20; Oct. 23).
　Piestopleura n. sp. (Aug. 13).
Belytidae:
　Xenotoma sp. (Aug. 20).
Diapriidae:
　Belyta sp. (May 7).
Serphoidea:
　Calliceras sp. (May 21; July 2; Aug. 6).
　Aphanogmus sp. (June 4; Aug. 6).
Formicidae:
　Monomorium minimum (Buckley) (Aug. 13; Oct. 6, 16, 27, 30).
　Myrmecina graminicola americana Emory (July 23; Oct. 2, 6).
　Prenolepis imparis (Say) (Nov. 28; Dec. 5, 12, 19; Jan. 2, 16, 23; Feb. 6, 20; Apr. 2, 16; May 14, 21, 28; June 4, 11, 18, 25; July 2, 9, 23; Oct. 9, 14, 16, 20, 27, 30; Nov. 6, 10).
　Leptothorax curvispinosus Mayr. (Jan. 2; May 7, 14, 21, 28; June 4, 11, 18, 25; July 16, 23, 30; Oct. 2, 27).
　Camponotus sp. (May 14; July 23; Oct. 6; Nov. 3).
Sphecidae:
　Stigmus sp. (July 30; Aug. 6).
Bethylidae:
　Chelogynus sp. (June 4).
　Aphelopus comesi Fenton (June 11, 18; July 16, 23).
Araneae:
Dictynidae:
　Dictyna foliacea Hentz (Oct. 2, 30).
　Dictyna sp. (prob. foliacea Hentz) (July 30; Aug. 20; Oct. 9, 14, 16; Nov. 3).
Scytodidae:
　Scytodes sp. (Mr. 5).
Theridiidae:
　Theridion sp. (prob. spiralis Emer.) (Nov. 28; Dec. 5; Jan. 2, 30; May 28; July 23, 30; Oct. 6, 9, 20, 30; Nov. 3, 6, 27; Dec. 25).
　Argyrodes sp. (Nov. 6).
　Dipoena sp. ? (July 23).
Linyphiidae:
　Linyphia sp. (July 23).
　Microneta sp. (Oct. 16).
Argiopidae:
　Leucauge hortorum Hentz (Mr. 5; Apr. 2; May 21; July 30; Oct. 2, 6, 9, 14, 16, 20, 23, 27, 30; Nov. 3, 17; Dec. 25).
　Araneus sp. (May 21; July 23, 30).
　Acacesia foliata (Hentz) (June 18; Aug. 20; Nov. 6).
　Mangora maculata Keys (May 28).
　Mangora sp. (July 9; Oct. 2).
Thomisidae:
　Tmarus caudatus Hentz (July 23, 30; Aug. 13, 20; Oct. 2, 14, 20; Nov. 6, 13, 27).
　Coriarachne versicolor Keys. (Nov. 28; Dec. 5; Feb. 13; Mr. 5).
　Xysticus sp. (Mr. 19).
　Synema parvula Hentz (July 30; Aug. 20).
Ctenidae:
　Ctenus sp. (Oct. 30).

Clubionidae:
　Anyphaena celer (Hentz) (July 16; Aug. 6, 13, 20; Oct. 14, 20, 27, 30; Nov. 3).
　Anyphaenella saltabunda (Hentz) (July 9, 16, 23, 30; Aug. 6, 13; Nov. 6).
Attidae:
　Dendryphantes octavus Hentz (Oct. 23).
　Dendryphantes nubilis Hentz (June 4; July 9; Oct. 20, 30).
　Dendryphantes sp. (Apr. 2, 16, 23; Oct. 2, 6, 9, 16, 20, 27; Nov. 13).
　Synemosyna formica Hentz (Oct. 6, 23).
Acarina:
Erythraeidae:
　Erythraeus sp. (July 9, 30).
Parasitidae:
　Parasitus sp. (July 30).
Ixodidae:
　Dermacentor variabilis Say (Feb. 13; June 11; July 2, 16).
Bdellidae:
　Bdella sp. (Oct. 20).
Trombidiidae:
　Trombidium sp. (May 14).
Miscellaneous:
　Atomus sp. (Oct. 23, 30).

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